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THE JOURNAL OF ECOLOGY

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THE ECOLOGICAL DISTRIBUTION OF BRITISH SPECIES OF *IDOTEA* (ISOPODA)

BY E. NAYLOR

Marine Biological Station, Port Erin

(With 4 Figures in the Text)

INTRODUCTION

Descriptions of the ecology of *Idotea* are often generalized, and there appears to be no comprehensive work on the habits of individual species. The present account of the ecology of *Idotea* in the Isle of Man, together with a discussion of relevant literature, includes extended observations on the commoner species, and illustrates that each species has a fairly characteristic range of habitat.

Collections were made on various types of rocky shore, and in some localities quantitative sampling was attempted with the aid of a wire frame enclosing an area of 0·1 m^2. Rock pools were examined, as were regions of the shore subject to the influence of freshwater streams. Surf plankton was collected by dragging a D-net along the edge of the sea on various sandy beaches, and the faunas of surface drift weed and buoys were sampled from a small boat. Dredgings were made off the south coast of the Isle of Man in depths down to about 10 fathoms. Both a naturalist's dredge and a D-net were used, the latter serving mainly to skim accumulations of algae, with accompanying *Idotea*, from a sandy bottom.

Seven species of *Idotea* were found in the Isle of Man—*I. emarginata* (Fabricius), *I. neglecta* G. O. Sars, *I. baltica* (Pallas), *I. linearis* (Pennant), *I. granulosa* Rathke, *I. pelagica* Leach and *I. viridis* (Slabber). Collinge (1917) records two other species from Britain: *I. metallica* Bosc. and *I. sarsi* Collinge. The first of these does not seem to be a British resident, the few specimens which have been recorded being chiefly found amongst *Lepas* on floating wood (Tattersall 1911), whilst the second, *I. sarsi*, is synonymous with *I. baltica*. I have examined the type specimens of *I. sarsi* in the British Museum, and they cannot be distinguished from *I. baltica* (Naylor 1955*c*).

SUBLITTORAL SPECIES

(*a*) Idotea emarginata

Bate & Westwood (1868) record *I. emarginata* from trawl refuse, and they state that the species 'is common all round the coasts of Europe'. Sars (1899) found it in abundance amongst decaying algae down to 20 fathoms, and Tattersall (1906, 1911) found it most commonly on *Laminaria* and floating algae. The *Plymouth Marine Fauna* (Marine Biological Association 1931) records *I. emarginata* as abundant in pools uncovered at half tide in Bovisand Bay, but Moore (1937) states that the species was most commonly trawled and only occasionally found on the shore.

In this investigation specimens of *I. emarginata* have been dredged from beds of

algae in and around Port Erin Bay (Fig. 1), and in particular from an accumulation of broken algae on a sandy bottom on the inner side of the ruined breakwater (Fig. 3). In addition, specimens were taken in surf hauls and on buoys in Port Erin Bay, and single specimens were collected on the shore.

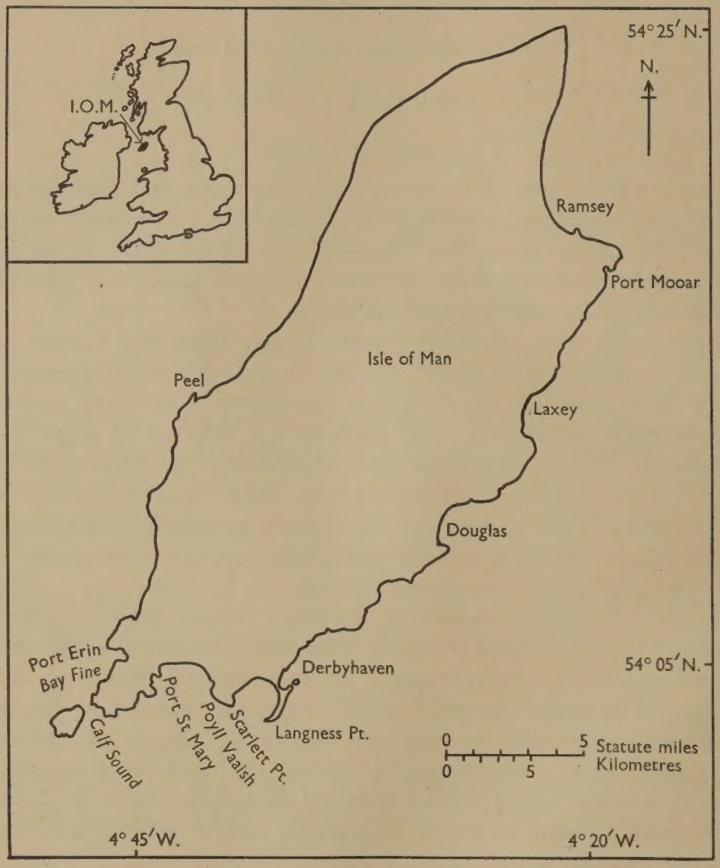

Fig. 1. The Isle of Man, showing localities where *Idotea* were collected.

The distribution and seasonal changes in the population of *I. emarginata* inside the ruined breakwater in Port Erin Bay are described elsewhere (Naylor 1955*b*). The bottom in that locality consists of sand and gravel, with scattered blocks of concrete from the breakwater itself, at a depth of 3–5 fathoms. Algae taken in the D-net hauls, kindly identified by Dr S. M. Lodge, included: *Laminaria digitata* (Huds.) Lamour, *L. saccharina* (L.) Lamour, *Saccorhiza polyschides* (Lightf.) Batt., *Desmarestia viridis* (Müll) Lamour, *Delesseria sanguinea* (Huds.) Lamour, *Ceramium* sp., *Plocamnium coccineum* (Huds.) Lyngb., *Myriocladia tomentosa* Crn., and *Odonthalia dentata* (L.) Lyngb.; some were living, but the bulk of the weed consisted of broken brown algae.

The *Idotea* were associated with the broken algae, and not with the living *Laminaria* as was suggested by Liao (1951). No *Idotea* were found on the *Laminaria* exposed at extreme low water spring tides.

I. emarginata seems to be essentially a sublittoral species, often associated with decaying algae, but it is to be expected that the species will often be washed ashore with such broken algae.

(*b*) Idotea neglecta

Sars (1899), Wahrberg (1930) and Elmhirst (1946) all found this species with decaying algae down to a depth of about 20 fathoms, and Sars associates the species with *I. emarginata*. Kjennerud (1950) in Bergen, found *I. neglecta* in large numbers at a depth of two to three fathoms where wood shavings and fish waste accumulated. Records of this species from the shore are given in the *Plymouth Marine Fauna*, Moore (1937) and Colman (1940).

In Port Erin Bay, during this investigation, *I. neglecta* was found with *I. emarginata* from inside the ruined breakwater. Specimens were found on *Laminaria* beds in Port Erin Bay and in Derbyhaven (Fig. 1), and they have also been taken in townettings in the Irish Sea (Mr A. B. Bowers). I have not found the species on rocky shores, but I have collected it in surf hauls over Port Erin beach and from buoys. Specimens collected on the shore have been sent to me from Dublin (Dr C. F. Humphries) and Belfast (Mr C. Edwards).

I. neglecta, like *I. emarginata*, is predominantly sublittoral, amongst decaying algae; it does not seem to be a resident shore species.

(*c*) Idotea baltica

Sars (1899), Tattersall (1906, 1911) and Nierstrasz & Steckhoven (1930) restrict *I. baltica* to 'shallow' or 'coastal' waters, often amongst floating algae. Specimens were trawled at Salcombe and collected with *I. emarginata* and *I. neglecta* in decaying algae washed ashore in the River Yealm estuary (Marine Biological Association 1931). Small specimens of *Idotea*, taken in hauls of surf plankton at Robin Hood's Bay, were chiefly *I. baltica* (Colman & Segrove 1955). In the Isle of Man Moore (1937) records the species as commonly trawled in Port Erin Bay and Bay Fine (Fig. 1), and he states that occasional specimens were found on the shore.

In this investigation a number of *I. baltica* were taken in dredgings in Port Erin Bay, both inside the breakwater and along the north side of the bay. The species was also taken in dredgings in Derbyhaven, and also on *Halidrys* at LWS in that region. Drift weed in hauls with a shore seine net at Peel yielded many specimens of *I. baltica*, as did surface drift weed at Port Erin. Small specimens are often taken in surf hauls, and I have taken single specimens on rocky shores at Scarlett Pt. and at Ramsey.

In some cases this species is associated with *I. neglecta* and *I. emarginata*, but it is more abundant on surface drift weed than those species. In this respect it is interesting to note that Dahl (1948) found few specimens of *I. baltica* in dredgings off the Swedish west coasts, and he took this as confirmation of his view that the species is associated with surface drift weed. Segerstråle (1944), however, associates the species with attached *Fucus vesiculosus* in the Gulf of Finland (see p. 267).

(*d*) Idotea linearis

Bate & Westwood (1868) found this species in dredgings and on the shore, in many British localities. Collinge (1917) also observed *I. linearis* on the shore, but Tattersall (1906, 1911) found it to be common in some Irish harbours, and often on floating weeds or timber. The *Plymouth Marine Fauna* records the species as common amongst *Zostera* on Drake's Island. I have regularly collected single specimens from dredgings in and around Port Erin Bay (see also Moore 1937), and some specimens have been taken in townettings in Morecambe Bay (Mr A. B. Bowers). I have found only one specimen in the intertidal zone, on the Queen's Pier at Ramsey. Records of *I. linearis* are few, and very few specimens were found in the investigation, but it seems that *I. linearis* is chiefly sublittoral, and is not a common shore species in the Isle of Man.

RESIDENT SHORE SPECIES

(*a*) Idotea granulosa

I. granulosa has often been confused with *I. viridis* (see p. 262) and with *I. neglecta* (see Kjennerud 1950). Sars (1899) and Wahrberg (1930) restrict *I. granulosa* to shallow water, King & Russell (1909) record it as the only shore idoteid in their investigations at Millport, and Moore (1937) records the species from crevices and pools on the shore at Port Erin. Packington (1934) working at Robin Hood's Bay, and Colman (1940) at Wembury, each found *I. granulosa* to be the only common shore idoteid, and Elmhirst (1946) observed the species with *Gigartina* on the shore. Kjennerud (1950) found it only on littoral fucoids in Norway. In the Isle of Man I have collected *I. granulosa* from algae on the shore at Port Erin, Port St Mary, Scarlett Pt., Derbyhaven, Laxey, Port Mooar, Ramsey and Peel (Fig. 1). In addition, I have collected and examined specimens from Flamborough and Plymouth, and have examined specimens from Robin Hood's Bay (Dr F. Segrove), Dublin (Dr C. F. Humphries), Belfast (Mr C. Edwards) and Skokholm (Miss E. C. Judges); all came from shore algae. *I. granulosa* occurs on buoys and in surface drift weed, but there is no doubt that it is mainly an intertidal form; it occurred only rarely in dredgings.

Monthly samples of seaweed from known levels on the shore were taken over a period of 15 months, with the object of determining which species of *Idotea* occur on the foreshore, and to study their distribution. (Observations on a wider range of rocky shores are described on p. 261; they compare the distribution of *I. granulosa* and *I. pelagica*.) A selected region of the shore surveyed by Southward (1953) at Port St Mary was used. Southward marked a stretch of limestone rock with a number of cement marks, and traverse *B–B* (see Southward 1953, Fig. 3) of these marks was used in the present investigation; the traverse extends from HWS to LWS. I am grateful to Dr Southward for supplying me with data on the positions of these marks. The shore is of gently shelving strata of limestone and it is exposed to moderate wave action (Southward 1953). The larger algae present were *Fucus spiralis* at HWN, *F. vesiculosus* at MTL, *F. serratus* and *Himanthalia elongata* at LWN, and *Laminaria digitata* at LWS.

A wire frame enclosing 0·1 m^2 was used in taking a representative sample of algae

from each station. *Idotea* were removed individually, while the weed in each sample was washed and sorted twice. Five times as many specimens were found in the first sorting as in the second, and it is assumed that most *Idotea* in the weed were removed in the two sortings. The damp weight of the weed in each sample was noted. Whenever possible, samples were taken monthly at HWS, HWN, MTL, LWN and LWS, and no sample was taken more than 5 yd from the traverse. All samples below HWS were of algae on the open shore, but at HWS a 1 lb jar was filled with *Enteromorpha* from pools.

Table 1. *Length-frequencies of* Idotea granulosa *amongst algae at each level sampled in 1953.*

	Tidal levels				
	HWS	HWN	MTL	LWN	LWS
Body length (mm)	*Enteromorpha*	*F. spiralis*	*F. vesiculosus* *Elachistea* sp.	*F. serratus* *H. elongata* *Laurencia* spp. *Cl. rupestris* *Ch. crispus*	*L. digitata* *Rh. palmata* *Cl. rupestris*
1–2	—	—	—	2	37
2–3	—	—	—	8	169
3–4	2	—	7	11	103
4–5	—	—	46	27	57
5–6	—	6	78	54	21
6–7	—	2	69	39	6
7–8	—	6	69	52	3
8–9	—	5	78	56	3
9–10	—	11	68	34	5
10–11	—	6	41	52	1
11–12	—	10	32	27	2
12–13	—	12	15	5	—
13–14	—	6	12	6	2
14–15	—	2	4	7	—
15–16	—	2	7	4	—
16–17	—	1	4	1	—
17–18	—	3	4	—	—
18–19	—	—	1	2	—
19–20	—	—	—	—	—
20–21	—	—	—	1	—
Totals	2	72	535	389	409

At LWS the *Laminaria* fronds were examined but no *Idotea* were found on them; only the holdfasts, with *Cladophora*, and the stipes, with *Rhodymenia*, were retained in the samples. It was not always possible to obtain a sample at LWS, particularly in winter, when low-water spring tides occur in the hours of darkness. *I. granulosa* was the only idoteid found in these samples over the whole 15 months. Specimens were present at each level sampled but they were most abundant at MTL and below.

All specimens collected in 1953 were measured to the nearest whole millimetre below their length, and the length-frequencies of all specimens from each level are given in Table 1. Small specimens were mainly concentrated below LWN, whilst the larger ones were most abundant farther up the shore. Specimens less than 5 mm long were most abundant at LWS on small algae such as *Cladophora* and *Rhodymenia*; those longer than 5 mm were found chiefly on fucoids, particularly *Fucus vesiculosus* at MTL. Hardly any specimens came from the *Laminaria digitata* itself.

Seasonal changes in the density of *I. granulosa* on the algae at each level are given in Fig. 2; fairly regular and similar trends are apparent at each level. The large specimens at MTL, and to a less extent at HWN and LWN, showed a marked increase in density during the autumn, falling off in density during the winter and early months of the year. Small specimens at LWS showed a similar trend, and they showed a maximum density in September.

Biological factors such as weed preference, as well as physical factors such as wave action and exposure to the air, affect the distribution of organisms living amongst seaweeds, and it is difficult to separate these factors in the case of *I. granulosa*. Large *Idotea* survive for greater lengths of time in reduced humidities because of their smaller surface:volume ratio, and because of this large specimens should be able to

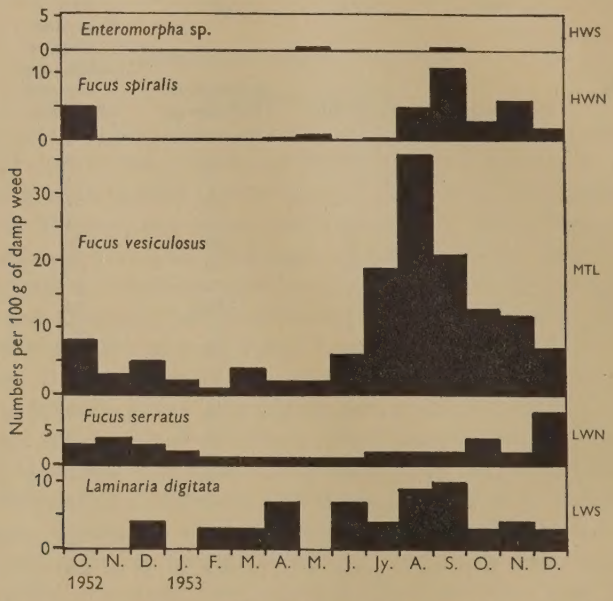

Fig. 2. The number of *I. granulosa* per 100 g of damp weed in monthly samples from five levels on the shore at Port St Mary. Figures for *Laminaria digitata* refer to stipes and holdfasts only. No sample could be taken at LWS in October or November 1952, or in January or May 1953.

extend farther up the shore than small ones, but this does not necessarily imply that small animals are always found below LWN as at Port St Mary. On more sheltered shores, where algal cover is more dense, small *I. granulosa* may extend to between MTL and HWN on *Polysiphonia lanosa*, the small tufted alga on *Ascophyllum* (Colman 1940). The preference for different types of algae by *I. granulosa* of different sizes seems to be at least partly dependent upon a choice of suitable food, and a choice of suitable foothold against tidal water movements. It is noticeable that *I. granulosa* of all sizes prefer shrubby algae; small specimens prefer small tufted algae such as *Cladophora*, whilst large specimens prefer the more branched fucoids, particularly *Fucus vesiculosus*; long, smooth fronded algae such as *Laminaria digitata* appear to be avoided.

(*b*) Idotea pelagica

Dollfus (1895), Elmhirst (1946) and Kjennerud (1950) found *I. pelagica* amongst *Balanus* and *Mytilus* on the shore, and Dollfus goes so far as to say that it is commensal with or parasitic on *Balanus*. Sars (1899) and Tattersall (1906, 1911), on the other hand, state that *I. pelagica* is associated with algae close to the shore. Dahl (1948) collected the species from localities which appear to be exposed to a great deal of wave action. In this investigation *I. pelagica* was found in material scraped from the Port Erin breakwater buoy (Fig. 3), from exposed shores near Port Erin, Peel and Port St Mary, and on the Queen's Pier at Ramsey. In all cases the species was amongst barnacles, *Mytilus* and stunted fucoids (particularly *F. vesiculosus* var. *evesiculosus*), in regions exposed to a good deal of wave action.

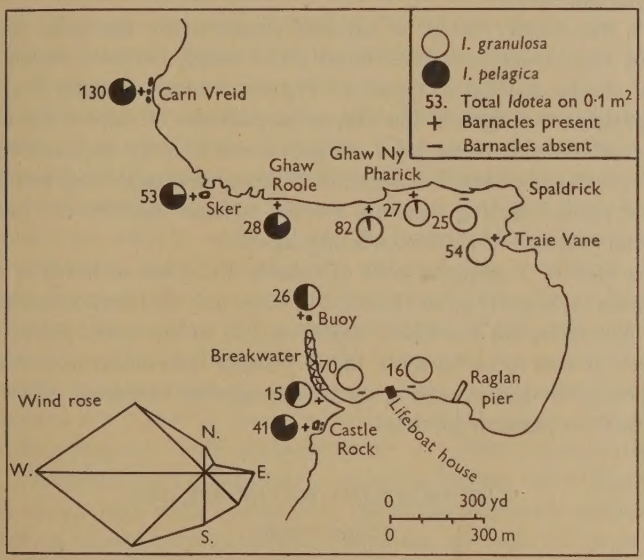

Fig. 3. The distribution of *I. pelagica* and *I. granulosa* in samples of 0·1 m² taken at MTL on shores in and around Port Erin Bay. The wind rose is derived by direct summation of 10-day means of wind speed and direction (June 1951–May 1953), issued by the Service Hydrographique, Charlottenlund, Denmark, and based on wind recordings at Ronaldsway Airport, some five miles east of Port Erin.

During 1952 and 1953 a shore survey was carried out to compare the distribution of *I. granulosa* and *I. pelagica* in and around Port Erin Bay. Some shores were reached on foot, but others were only accessible by rowing boat and on calm days. Samples were taken, as near as could be judged, at MTL, in the *Fucus vesiculosus* (or *Ascophyllum nodosum*) zone. All weeds and barnacles in an area of 0·1 m² were brought back to the laboratory, where all *Idotea* were removed and the dominant organisms noted. At the station on Castle Rock (Fig. 3) similar samples were taken at about HWS, HWN, LWN and LWS in a traverse down the shore. The levels were determined approximately, from the level of predicted low water on a calm day. The prevailing winds are westerly and the outer parts of the area sampled are exposed to a great

deal of wave action. The region inside the breakwater receives some shelter, and a decrease in exposure eastwards towards Spaldrick, along the north side of the bay, is apparent from observation. This decrease has been demonstrated qualitatively by Southward (1953).

I. pelagica and *I. granulosa* were the only idoteids found in this shore survey the results of which are shown in Fig. 3. *I. pelagica* was the dominant *Idotea* in the outer parts of the region sampled, where wave action was greatest and where barnacles were largest and most abundant. On more sheltered shores, where algae were dense and barnacles sparse or absent, *I. granulosa* predominated. In the traverse on Castle Rock forty-six out of a total of forty-seven specimens of *I. pelagica* were taken at HWN and MTL, where barnacles were dense. There were fewer *I. granulosa* in the samples (only fourteen in all), but these were found amongst algae as at Port St Mary (see p. 259), mainly at MTL and below.

I. pelagica was mainly found on exposed shores where barnacles were present. Furthermore, most specimens were found inside empty barnacle shells, so that, on less exposed shores, such as at Ghaw ny Pharick, where barnacles were small and flat, few *I. pelagica* were found. But despite its tolerance of wave action and its close relationship with suitable barnacles, *I. pelagica* seems to avoid the most exposed parts of the shore which completely lack algae, even though barnacles may be present. It is probable that regions lacking algae are avoided because they dry out too quickly at low water; the presence of algae retards drying out.

As for the food of *I. pelagica*, cells of fucoids and parts of barnacle appendages have been found in the gut (Naylor 1955*a*). The latter may well have come from damaged or moulted barnacles, but the *Idotea* might be able to bite small pieces from living barnacle cirri. It does seem, however, that *I. pelagica* is an omnivorous scavenger like other members of the genus, seeking shelter amongst the barnacles, rather than being commensal with or parasitic on them.

THE BRACKISH WATER SPECIES

Idotea viridis

I. viridis often appears to have been confused with other species, particularly *I. granulosa*. Accepted texts for identification (Sars 1899, Collinge 1917, Nierstrasz & Steckhoven 1930) give no ecological details, but many workers agree with present observations that *I. viridis* is a brackish water species (Dollfus 1895, Norman 1904, Tattersall 1911, Crawford 1937, Spooner & Moore 1940, Howes 1939*a*, Dahl 1944, 1948, Forsman 1951). In contrast Elmhirst (1946) associates large specimens of the species with *Ascophyllum* and immature ones with *Cladophora*, and Watkin (1941) suggests that the species is seasonally migratory between littoral and sublittoral algae in Kames Bay. These authors appear to have confused *I. viridis* with other species, possibly *I. granulosa* and *I. baltica* respectively. Apart from Manx specimens I have seen *I. viridis* from Holbeach (Lincs.), Langton Herring (Dorset), Tamar Estuary (Devon and Cornwall) and Great Wakering (Essex) sent to me by Mr G. M. Spooner, and from Little Cumbrae Island (Bute) sent to me by Dr R. B. Pike. All these specimens came from brackish water.

The *Marine Fauna of the Isle of Man* (Moore 1937) records *I. viridis* several times from Port Erin Bay, but these records are open to some doubt. Two specimens collected in Port Erin Bay and retained in the faunal collection as *I. viridis* are, in fact, *I. granulosa*. Moreover, since the details of habitat accompanying previous records do not agree with what is now known of the ecology of *I. viridis*, it may be suggested that the early records referred to some other species, and that so far as is known the finding of *I. viridis* in this investigation constitutes the first true record of the species in the Isle of Man. Specimens have been found in two brackish pools near Poyll Vaaish, in a similar pool on Langness Pt., and in two connected pools at Scarlett Pt. (Fig. 1). The two pools at Poyll Vaaish and the one at Langness are similar in many ways. All three are quite large (the smallest measures about 10 ft by 5 ft) and all are situated beteeen HWN and HWS on gently shelving, sheltered shores. The pools are permanent, each receiving fresh water, by seepage, as at Poyll Vaaish, or by a definite stream, as at Langness, and each is reached by the sea during the higher tides. Salinity of the pools varies markedly with the state of tide, wind strength and direction, and rainfall. Each pool has a vegetation of large green algae (p. 264).

The pools at Scarlett are situated higher than those already described, but, as will be shown below, they are ecologically similar. They are at the head of a deep gulley in an exposed part of the shore, and the lower pool opens to the gulley by a narrow crevice 5 ft above MHWS. Provided there is sufficient swell the funnelling action of the gulley causes sea water to be forced into the lower pool at all states of tide above about HWN, and during storm conditions the two pools may be merged. Fresh water flows through the pools from a stream farther inland. Salinity in the pools varies widely and irregularly, because of the sporadic effects of both salt and fresh water. The upper pool is only about 6 in. above the lower one, but sea water entering the lower one does not always reach the upper one. Even so the range of salinity is high in the upper pool and it may be correlated with the phase of tide. Samples taken on different visits to the pool, kindly analysed by Mr D. J. Slinn, showed that the lowest value (6·8‰) occurred during neap tides, whilst the highest value (29·5‰) occurred immediately after a high water spring tide. These two values are not necessarily the extreme limits of salinity range in the pool. If neither sea water nor fresh water enters a particular part of the pools for some length of time, evaporation may raise the salinity to a value above that of sea water. On 12 May 1953 sea water entered the lower pool near the gulley, but it had little effect on the salinity of the water at the western end of the pool some 15 ft away; no fresh water entered on that day. The salinity at the western end of the pool, where it was shallow, rose from 36·0 to 38·6‰ in the six hours after high water. Near the gulley, where sea water entered around 1000 h G.M.T., salinity ranged only from 34·3‰ at 1000 h to 34·7‰ at 1600 h. Thus salinity may vary seasonally, daily, and even spatially within the pools.

Temperature ranges in the pools may be great because of the effect of fluctuating air temperature on such small masses of water, but any such ranges are often alleviated by the influx of sea water. On 12 May 1953 temperatures at a depth of 9 in. were noted over a period of six hours from high water. Near the mouth of the gulley, where sea water entered at 1000 h, the temperature rose from 9·1° C (that of sea water) at 1000 h, to 15·5° C at 1600 h. At the western end of the pool sea water had little

effect at high water and the temperature rose from 15·5° C at 1000 h to 22·2° C at 1600 h. The day was sunny, but with some breeze; air temperature in the breeze rose from 11·4 to 16·4° C over the six hours.

Oxygen concentrations of samples also taken on 12 May 1953 were lower in the morning than in the evening, presumably in accordance with the photosynthetic and respiratory activities of the algae in the pool (see below). Where the pool was undisturbed by sea water, oxygen concentrations rose sharply from the low value of 2·83 ml/l. at 1100 h to 12·22 ml/l. at 1600 h. Near the mouth of the pool sea water entered at 1000 h and oxygen concentration was 6·5 ml/l. (about that of sea water) at that time; it rose to 10·00 ml/l. in the next six hours.

The biological features of the pools have been studied in some detail, and these may now be described. Three species of algae (all Chlorophyceae) formed three zones around the sides of the pools. *Enteromorpha intestinalis* formed the upper zone, which extended between the pools, *Chaetomorpha aerea* the middle zone, and *Cladophora rupestris* the lowest zone, and the last species was particularly abundant in the deeper parts of the pools. In the crevice between the lower pool and the sea the *Enteromorpha* and the *Chaetomorpha* were absent, but the *Cladophora* was profuse.

Collections of the fauna were made in May 1953 and January 1954. Species taken on both occasions include *Procerodes ulvae* (Oersted), *Littorina saxatilis* (Olivi), *Gammarus duebeni* Lilljeborg, *Jaera nordmanni* (Rathke), *J. albifrons* Leach, *Ligia oceanica* (L.) and *Idotea viridis*. Other species collected during the summer were *Leander serratus* (Pennant), *Carcinus maenus* (Pennant), *Gasterosteus aculeatus* L. and chironomid larvae; whilst additional species in winter included *Gammarus locusta* (L.) and *Melita palmata* (Montagu). At the seaward end of the crevice in May were *Procerodes ulvae*, *Jaera albifrons*, *Gammarus duebeni*, *Hyale prevosti* (Milne-Edwards) and *Littorina saxatilis*, but no *I. viridis* were present.

It is clear that purely marine organisms will often be washed into the pools even though they may not survive; *I. viridis* was the only idoteid found in the pools.

As has been stated, several writers describe *I. viridis* as a brackish water form, and these observations agree. However, as Forsman (1951) points out for *Gammarus duebeni*, it only applies in so far as *I. viridis* is found in marine habitats more or less influenced by fresh water. It is not true to say that *I. viridis* (or *G. duebeni*) is physiologically dependent upon brackish water (as will be demonstrated later, on p. 265), nor is it necessarily found in water which is permanently brackish. The common features of the Manx localities where *I. viridis* occurs appear to be: a sheltered, permanent pool with a sporadic supply of both salt and fresh water, and a vegetation of the larger green algae. These features conform with the habitat of *I. viridis* on Little Cumbrae Island (Dr R. B. Pike, personal communication), though the habitat described by Howes (1939*a*, *b*) seems to be subject to rather less salinity changes than those described for the pools at Scarlett. In the river Tamar (Crawford 1937, Spooner & Moore 1940) salinity changes do occur, and the association of *I. viridis* with green algae or *Zostera* is noted by Spooner & Moore.

ECOLOGICAL ADAPTATION AMONGST *IDOTEA* SPECIES

Some experiments have been carried out to determine how different *Idotea* species react to conditions designed to simulate various environmental factors.

(*a*) *Resistance to changes in salinity*

Ranges of salinity tolerance have been worked out for *I. viridis*, *I. granulosa*, *I. pelagica* and *I. emarginata*. Solutions were made up from filtered sea water diluted with distilled water or concentrated with Tidman's Sea Salt. 2000 ml of each of the following solutions were made up: 0, 12·5, 25, 50, 75, 100, 112·5, 125, 150, 175 and 200 % sea water; salinity therefore ranged from 0 to 70‰. Fresh solutions were made up at intervals. All *Idotea* were kept in sea water and were used as soon as possible after capture. Five specimens of one species were placed in each solution, and the condition of the specimens was noted every few hours. The specimens were removed

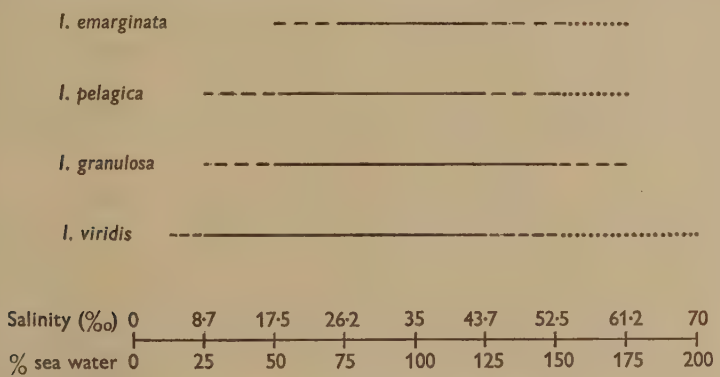

Fig. 4. Ranges of salinity toleration of four species of *Idotea*, after 48 h under experimental conditions (——, over 80 % healthy survival; - - - -, less than 80 % healthy survival; . . . ., a few surviving, but comatose).

when their condition had been constant for some hours (usually after about 48 h), and the experiment was repeated with each species in turn. All four series of experiments were carried out a second time with other specimens of each species, and there were no major discrepancies between the two sets of experiments. Temperatures ranged from 10–14° C, depending on when the experiment was carried out, but the temperature during any one experiment never varied by more than one degree Centigrade altogether.

I. viridis survived longer in reduced salinities than the other three species (Fig. 4), and the lowest salinity tolerated by *I. viridis* in these experiments agrees closely with that described for Swedish specimens, namely 4–6‰ (Dahl 1944). The shore species *I. pelagica* and *I. granulosa* will be subject to the influence of rainfall on the shore, and it is significant that they have a lower limit of toleration than the sublittoral species *I. emarginata*. The position is less clear-cut in the higher salinities, but certainly some *I. viridis*, and no other species, were alive, though comatose, after 48 h in 200 % sea

water. Indeed, some *I. viridis* were alive, though torpid, after four weeks in open dishes (with food), from which water had been allowed to evaporate and the salinity raised to more than twice that of sea water; this was not tried for other species. *I. viridis* is clearly a markedly euryhaline species; it tolerates lower salinities than other species, and no others survived for any length of time in 200% sea water.

(*b*) *Resistance to desiccation*

The shore idoteids *I. granulosa* and *I. pelagica*, unlike the sublittoral and brackish water species, are periodically exposed to the air, and it is of interest to study this as a factor limiting the distribution of the various species.

When placed in constant humidity chambers, in which humidity was controlled by the use of sulphuric acid solutions (Williamson 1951), it is found that the shore species show no appreciably higher resistance to desiccation than a sublittoral species, *I. emarginata*, or the brackish water species, *I. viridis*. Field observations tend to bear this out since *I. granulosa* shelters in wet weed when the tide is out and *I. pelagica*, though inhabiting barnacle shells on exposed coasts, seems to prefer the presence of some algae (see p. 262), presumably for the moisture which the latter retain. It seems, therefore, that exposure to the air is an absolute limiting factor for all species, and that it is some factor other than tolerance of exposure to the air which allows the shore species to inhabit the intertidal zone which the other species seem unable to colonize.

(*c*) *Possible structural adaptations*

The relation between ecology and body form of organisms in seaweeds has been discussed by several authors (see Dahl 1948), and there may be some relation between wave action and the morphology of *Idotea*. Those species which are tolerant of wave action, *I. pelagica* and, to a less extent, *I. granulosa*, are more robust and have stout appendages, which are less liable to be broken and which enable the *Idotea* to cling on more strongly. *I. pelagica* is subject to greatest wave action and it has the shortest antennal flagellum of any species studied (Naylor 1955*c*), besides having the largest claws. Perhaps it is inability to tolerate wave action which precludes sublittoral species from inhabiting the intertidal zone.

DISCUSSION

Idotea occur mostly amongst algae and, since shore algae may be washed away from the intertidal zone and sublittoral algae may be washed ashore, some mixing of sublittoral and littoral *Idotea* must take place. Wherever possible, therefore, extended observations must be made on resident breeding populations, if specific environments are to be determined.

Distinct environments are attributable to the following species: *I. viridis*, in brackish water; *I. granulosa*, amongst algae in the littoral zone, in moderate shelter; and *I. pelagica*, on exposed coasts amongst barnacles. Laboratory observations show that *I. viridis* is better able to tolerate reduced salinities than other species, and it does seem that the shore species are better adapted, structurally, to withstand the mechanical effects of wave action.

The distribution of the sublittoral species is less clear, but present observations on *I. emarginata* and *I. neglecta*, and those on *I. neglecta* in Norway (Kjennerud 1950) agree in suggesting that these two species are associated with decaying organic matter (see also Sars 1899, Elmhirst 1946). Kjennerud found *I. neglecta* on decaying animal matter, whereas *I. emarginata* was found amongst broken algae at Port Erin, but no valid generalization may be made from these observations; *I. neglecta*, for example, is often found together with *I. emarginata* on decaying algae (p. 257). No published work can be found on breeding populations of the two other sublittoral species, *I. baltica* and *I. linearis*, and further work is necessary, particularly with regard to the suggestion that *I. baltica* is associated with surface drift weed.

It may be that all species are potentially capable of survival in the sub-littoral zone, where conditions are fairly uniform. But, as Forsman (1951) points out when dealing with *Gammarus duebeni*, 'a very variable and therefore difficult and hazardous environment can only be mastered by especially hardy species', and the restriction of a species to a particular region, with exclusion from other habitats which it could tolerate, is possibly due to biological factors such as competition (see also Beadle & Cragg 1940, Jones 1948). Such factors may restrict *I. pelagica* and *I. viridis* to their respective rigorous environments.

These conclusions apply to Manx, and probably to other British specimens as well, but to what extent they apply to other regions is not clear. On the west coast of Sweden, where conditions are almost fully marine, *I. viridis* is a brackish pool species (Forsman 1951), and *I. baltica* seems to be associated with drift weed (Dahl 1944). In the Gulf of Finland, however, *I. viridis* is an open water form and it extends, with *I. granulosa* and *I. baltica*, into regions where salinity is permanently below 10‰; *I. baltica* is there associated with attached *Fucus vesiculosus* (Segerstråle 1944). Not only is salinity low in that region, but tidal influence is negligible, and several organisms appear to have different habitats from specimens of the same species in fully marine conditions.

ACKNOWLEDGEMENTS

Apart from people mentioned in the text I am grateful to Mr J. S. Colman for his criticism of the manuscript.

SUMMARY

1. Manx *Idotea* are divided into three groups on an ecological basis: (*a*) *I. emarginata*, *I. neglecta*, *I. baltica* and *I. linearis* are predominantly sublittoral, down to about 10 fathoms, amongst decaying and living algae; (*b*) *I. granulosa* and *I. pelagica* are shore species, the former amongst *Ascophyllum* and *Fucus*, and the latter on exposed shores, where it shelters in empty barnacle shells; and (*c*) *I. viridis* inhabits brackish pools at HWN and above. The horizontal and vertical distribution of the last three species are discussed in some detail.

2. Experiments were carried out to test the adaptation of the various species to environmental factors such as salinity and humidity, and ecological adaptation amongst the species is discussed.

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THE LIFE CYCLE OF THE ISOPOD *IDOTEA EMARGINATA* (FABRICIUS)

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(With 8 Figures in the Text)

INTRODUCTION

Until recently no work appears to have been done on breeding populations of *Idotea*; there are few published data on the growth and reproduction of the several species, but Howes (1939) and Kjennerud (1950) have made studies of *I. viridis* and *I. neglecta* respectively.

A large population of *Idotea* occurs at a depth of three to five fathoms on the inner side of the ruined breakwater in Port Erin Bay, Isle of Man. The position and density of the population in the summer of 1952 (Fig. 1) was determined by a series of ten intersecting hauls with a D-net, each haul lasting 5–10 min; the total *Idotea* in each haul were estimated as less than 100, 100–1000, or more than 1000. The bottom there consists of sand and gravel, with scattered blocks of concrete from the ruined breakwater. There is often an accumulation of broken brown algae in the region (Naylor 1955*a*), and the *Idotea* were most abundant when large quantities of such weed were present in the hauls. Five species of *Idotea* were taken, but out of 7793 specimens examined, *I. emarginata* formed 97 %, *I. baltica* and *I. neglecta* comprised the bulk of the remaining 3 %, whilst *I. linearis* rarely occurred more than once in any one sample. One specimen of *I. granulosa* was taken.

Monthly samples were obtained throughout 1952 and 1953 by means of a D-net towed from the 30 ft motor boat *Cypris*. The D-net was preferred to a naturalist's dredge since it effectively collected weed and *Idotea* without digging up the sand or gravel (Jones 1948). The net was shot near the base of the breakwater and towed northwards parallel to the breakwater for about 200 yd. In June 1952 the motor boat was under repair and the sample was obtained using a smaller D-net from a dinghy.

All weed in the D-net was retained, and the *Idotea* were removed alive. Weed was sorted and washed under a continuous flow of sea water into a bath, and the idoteids swimming free were decanted off at intervals into a fine sieve. If sand was present, a coarse sieve (2 mm) was used to separate the sand and smallest *Idotea* from the weed; the smallest *Idotea* were then decanted from the sand. Specimens were killed in formalin and preserved in Baker's calcium formol or in 5 % formalin in sea water. Subsamples were taken by spreading the specimens evenly in a dish in water, draining off the water by gently tilting the dish, and halving the sample. This procedure was repeated, usually until about 200–400 specimens remained.

All specimens in the subsample were measured, and those of 7 mm or more were sexed (external genitalia are recognizable only after a length of about 7 mm is attained). In females the presence or absence of a brood pouch was noted and, if a brood pouch

contained embryos, the state of development of these was also noted. The aesthetascs on the antennules of individuals in the 1952 samples were counted, and in some samples the number of segments on the antennal flagellum also. Measurements of body length were taken down the mid-dorsal line, whilst the animal was slightly flattened. Specimens of 7 mm and over were measured against a non-parallax scale under a low-power binocular microscope, and specimens of less than 7 mm in length were measured

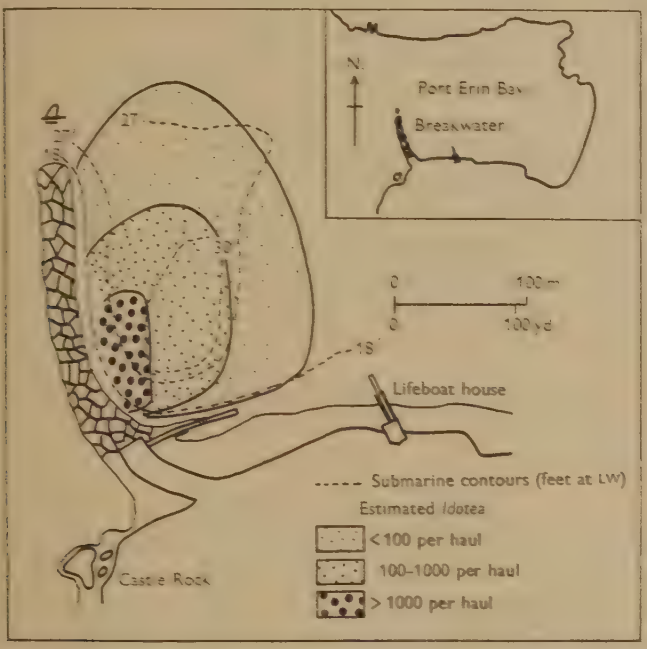

Fig. 1. The distribution and density of the population of *I. emarginata* inside the breakwater in Port Erin Bay, as determined in the summer of 1952.

under a monocular microscope fitted with a micrometer eyepiece. Measurements were made to the nearest 0·1 mm, but in most cases the lengths are given here to the nearest millimetre below.

The quantitative value of the samples is limited because it was not always possible to sample along the same line each month. Except in very calm weather it was difficult to approach very near to the breakwater, and there was always the possibility of the net being fouled on a block of concrete, with subsequent deviation in the sampling line. Furthermore, the laying of crab pots by local fishermen sometimes impeded sampling. As far as can be judged, however, the samples and subsamples were not selected and are therefore at any rate of qualitative value.

DEVELOPMENT, GROWTH AND REPRODUCTION

(*a*) *Marsupial development*

Early development takes place within the brood pouch of the adult female, the eggs being shed into the marsupium after internal fertilization. Four distinct developmental stages are recognizable within the brood pouch, and each stage is separated by a larval ecdysis. This closely follows the description of marsupial development given for *I. neglecta* (Kjennerud 1950), and also for *Jaera albifrons* (Forsman 1944).

The first marsupial stage occurs within the egg membrane. The eggs are spherical at first, with a diameter of about 0·7 mm, and they are green in colour, like those of *I. neglecta* (Kjennerud 1950). As development proceeds the eggs become ovoid and the egg membrane ruptures to release the second stage.

The second marsupial stage is enclosed by what Kjennerud calls the embryonic membrane. The embryo is now elongated and is about 1·2 mm long; it segments and the appendages appear beneath the embryonic membrane, which then ruptures.

The third marsupial stage has fully formed appendages but these lack any trace of setae. The length of the embryo at this stage is about 1·8 mm.

The fourth marsupial stage appears after a third moult has taken place; at this stage the embryos escape from the brood pouch as 'newly released juveniles' (see below).

In the brood pouch of one female, the whole development of the embryos up to the time of release took place in 30 days at 9° C in the laboratory.

(*b*) *Post-marsupial development*

Newly released juveniles (Fig. 2) range in length from 2·0 mm for those released in September, to about 2·3 mm for those released in the early months of the year (Fig. 3). The head is relatively larger than in the adult, and the broadest part of the body is across the first thoracic segment. The antennule bears two aesthetascs at its tip, and the antennal flagellum consists of two segments. Only six pairs of legs are present at this stage, the seventh thoracic segment being small and devoid of limbs. Furthermore, as in newly released juveniles of all species of *Idotea*, the telson is bluntly rounded (Fig. 2) and is not emarginate across its posterior border as it is in the adult. Specimens at this stage moulted after 14 days when reared in the laboratory at 10° C.

The second free-living stage is about 2·6 mm in length (though spring specimens are larger than those released in the autumn) and the antennal flagellum increases to a length of about 0·34 mm. Otherwise this stage resembles stage I; the antennal flagellum still consists of two segments, the antennule bears two aesthetascs, the seventh pair of legs has not yet appeared, and the telson is still rounded at its tip. But despite the similarity with the first stage, the length of the antennal flagellum and the body length measurements aid in separating the two groups. Fig. 3 shows the length frequencies (in 'micrometer eyepiece units') of all specimens in 1952 which had two aesthetascs on the antennule; some of the histograms, particularly those for May and September, are distinctly bi-modal, clearly distinguishing the first two stages. Also, as has been pointed out earlier, the modal sizes of the two groups are

shown to be less in summer and autumn than in the early months of the year. Animals in the second stage again moulted after about 14 days at 10° C.

The third stage is about 3·3 mm in length, and it is quite distinct from any other stage; it is characterized by the presence of a pair of half-formed legs on the seventh thoracic segment. This pair of legs is usually folded forwards beneath the sixth pair of legs. The antennule bears three aesthetascs and the antennal flagellum shows a

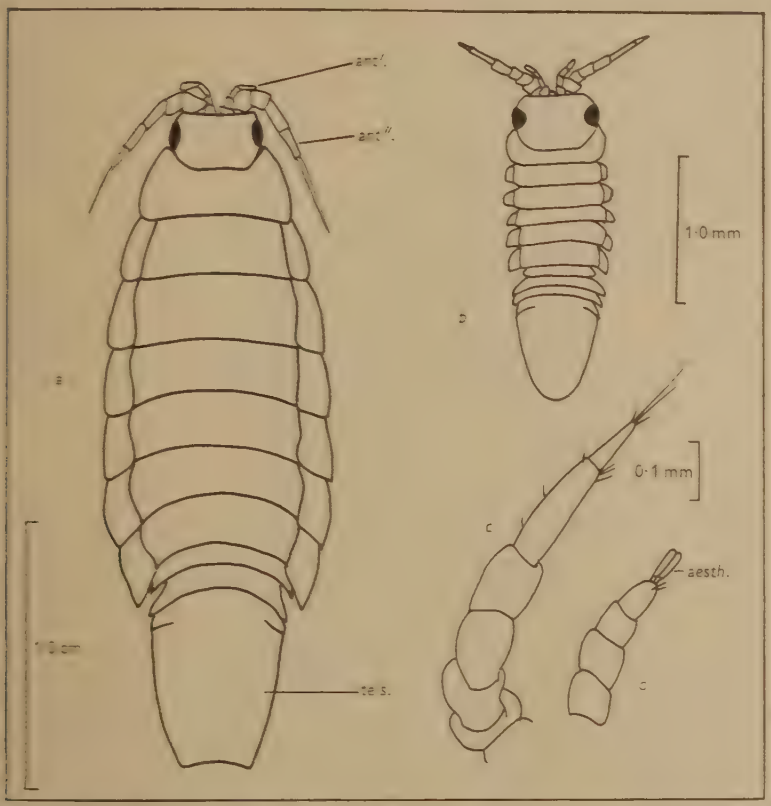

Fig. 2. *a*, An adult male *I. emarginata*, from above (*ant.'*, antennule; *ant.''*, antenna; *tels.* telson). *b*, Newly released juvenile *I. emarginata*, with its antenna (*c*) and antennule (*d*) further enlarged.

further increase in length, though it still consists of only two segments. The telson is slightly straightened across its posterior border, but it is by no means emarginate. This third stage again moults after about 14 days, and corresponds to the second stage in *I. neglecta* described by Kjennerud (1950).

Subsequent growth stages are difficult to separate, since characters change less regularly at each succeeding moult. The last pair of legs is acquired after the third moult and so no longer serves as a distinguishing character. Furthermore, as the length of the body increases, the addition of aesthetascs (Fig. 4) and antennal segments is irregular, and it is difficult to subdivide the growth into distinct stages on these

characters. Aesthetascs are acquired, at first singly but later usually in pairs, away from the tip of the antennule (Naylor 1955 *b*), but even though they may be acquired singly they are always eventually arranged in pairs, any single aesthetasc being added to at the next moult. The segments of the antennal flagellum are budded off from the basal segment and the number of segments approximates to that of the aesthetascs of the antennule. The posterior end of the telson first becomes concave when specimens reach a length of about 7 mm, and it soon acquires its adult shape (Fig. 2).

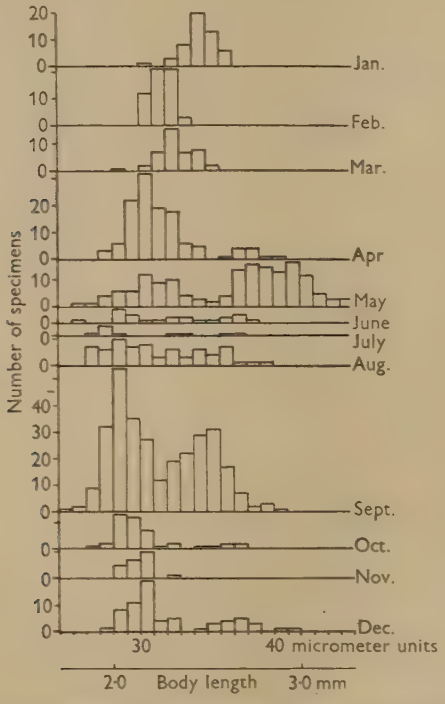

Fig. 3. Length frequencies of all specimens having two aesthetascs on each antennule which were taken in 1952.

No external sexual characters are visible until a specimen is at least 7 mm in length (Fig. 4). A few males are recognizable at this length, and most males are recognizable when they are 8 mm long. At this stage the paired penes, on the mid-ventral surface of the first abdominal segment, are small; the appendix masculinus, developing from the inner ramus of the second pleopod, has not yet acquired its adult shape (Naylor 1955 *b*). Over successive moults, the penes increase in length and the appendix masculinus becomes completely separated, except at its base, from the inner ramus of the pleopod. Once the appendix masculinus has acquired its adult shape it grows less quickly than the pleopod.

An additional feature characteristic of males is the appearance of pads of fine setae on the inner surfaces of the joints of the second pair of legs. The male holds the female

with this pair before copulation, and the setae would seem to provide a good grip on the smooth surface of the female's body.

Some males mature when they are about 10 mm long, and all males continue to grow throughout life; a few reached almost 30 mm and had up to sixteen aesthetascs on their antennules in 1952 (Fig. 4).

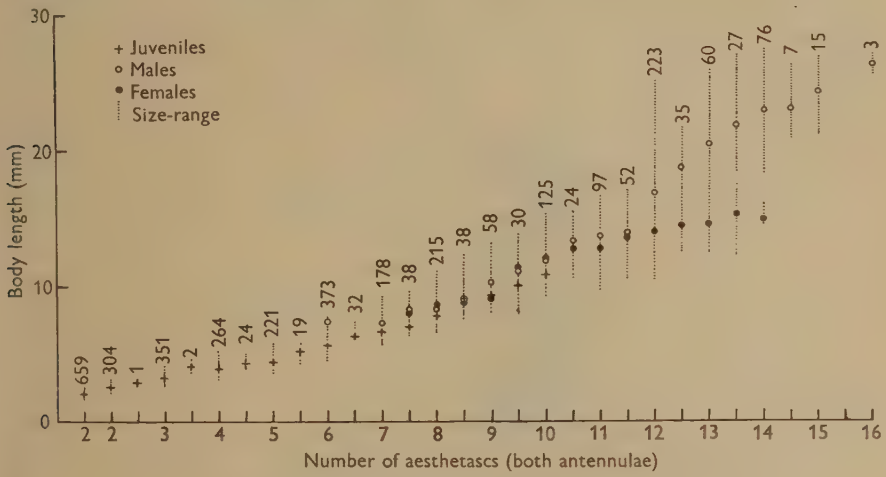

Fig. 4. The mean size, size-range and total specimens in each aesthetasc group, calculated from all specimens in 1952 samples.

Immature females are recognizable before they acquire oostegites, since they bear small flaps containing the developing oostegites at the bases of the first five pairs of legs. At maturity when the oostegites appear, the body of the female becomes relatively broader than that of the male and, whereas the male is broadest at the sixth thoracic segment, the female is broadest at the third. In addition, a small lappet develops on the coxa of the maxillipede and projects into the marsupium; this structure is used in creating a current of water through the brood-pouch (Naylor 1955 *b*).

In the summer months of 1952 and 1953 immature and mature females from Port Erin Bay were small, mostly 7–11 mm long, but from December to April they ranged from 10 to 17 mm (Fig. 5). One main stock of *I. emarginata* matured in the summer, and the other from October to December (p. 277), so it seems that those growing in the summer matured at a smaller size than those maturing later in the year.

(*c*) *Rate of growth*

Newly released juveniles were present in most of the samples taken (p. 276), and because of this it is difficult to determine the growth-rate from the samples. An attempt was made to rear *I. emarginata* in aquaria but none survived for more than 90 days, by which time they had grown to a length of 10 mm (temperature rose from 11 to 16° C during the course of the experiment). Beyond this no comparable data are available, but there is some evidence that there is a different pattern of growth in older males and females.

Of specimens of *I. emarginata* with twelve or more aesthetascs on each antennule, females are smaller in size and fewer in number than males (Fig. 4). It seems, therefore, that not only do females have fewer moults than males, but unlike males they cease to grow during the later moults. This partly conflicts with observations on *I. neglecta*, in which, though males have more moults than females, there appears to be no slowing down of growth of the females (Kjennerud 1950) because 'both males and females...possessing the same number of sense rods on the antennule, have the same mean size'.

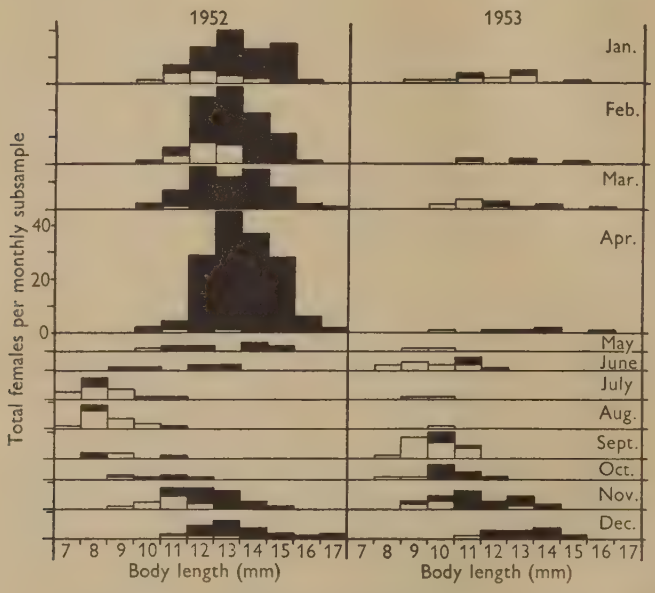

Fig. 5. The size-range of females in each monthly subsample, in 1952 and 1953 (□ females without brood pouch, ■ females with brood pouch).

(*d*) *Reproduction*

Some breeding takes place all the year round and newly released juveniles, mostly in the 2 mm group, were present in all samples taken during 1952 and 1953 (Fig. 6). It is apparent, however, that breeding was limited at certain times of the year; the presence of newly released juveniles fell off in the summer months of both 1952 and 1953 (Fig. 6), and the abundance of females with advanced embryos or emptied brood pouches showed a similar decline (Fig. 7).

The breeding behaviour of *I. emarginata* is similar to that in other isopods (see Kjennerud 1950). Males pair with females which will acquire oostegites at their next moult, and copulation takes place as the female moults. Sperm is transferred from the penes to the female oviducts by the appendix masculinus of the male, and after fertilization the eggs are released into the brood pouch formed by the newly released oostegites.

Howes (1939) noted a reduction in the number of embryos of *I. viridis* as they got older, and in the brood pouch of some individuals he found embryos in different stages of development. Neither of these characteristics was observed in *I. neglecta* (Kjennerud 1950) nor in *I. emarginata* in this investigation. Forty female *I. emarginata* with embryos in all stages of development were examined, but in any one brood pouch the embryos were all at one stage of development; no marked falling-off in the numbers of embryos in successive stages of development was observed.

Kjennerud (1950) states that *I. neglecta* in Norway has only one brood, but *I. emarginata* in Port Erin Bay may have had more than one brood. Certainly those specimens which matured and released young in the autumn, continued to grow in the later months of the year. Males and females captured in September and kept in aquaria all died after one brood had been produced, but it is not known whether they would have done so in their natural habitat.

SEASONAL CHANGES IN THE POPULATION

The frequency of *I. emarginata* in each millimetre size-group for each of the months sampled is given in Fig. 6. Large specimens were fewer in the early months of 1953 as compared with 1952, but in general the size composition of the samples followed a similar pattern each year. From January to April in 1952 the size ranged up to nearly 30 mm. The population at this time consisted chiefly of a great number of newly released juveniles in the 2 mm group, adult females ranging from 10 to 17 mm, and males ranging from 12 to 27 mm. The adult males and females gradually decreased, presumably dying off, until they had almost disappeared in May. At the same time more and more newly released juveniles were present in the samples, and they showed no signs of growth until the adults had disappeared in May.

The juveniles released in the early parts of the year grew from May to August, at which time some matured and produced young, the 2 mm group thereupon showing an increase in numbers. In the three months from June to August no specimens longer than 13 mm were present in the samples, since all the large over-wintering males and females had disappeared. The slight peak in the 2 mm group in August became very marked in September and October. At the same time the upper size limit of specimens in the samples began to increase again, suggesting that at least some of those which had matured in August continued to grow. The individuals released in September and October began to grow in November, and there was a proportional fall in the numbers of juveniles being released. The size-range in the whole sample continued to increase, and it almost reached that of the samples in the early months of the year. The size-range in December was large, and the numbers in the 2 mm group began to increase again. It appears as though this sample consisted of three main generations: large males and females which began growth in May, maturing individuals which were released in September, and a number of newly released juveniles.

In 1953, though the general pattern of variation in the population is similar to that in 1952, there are some differences. Between January and May the two older over-wintering groups released young and disappeared from the samples. These larger specimens were fewer than in 1952, but what few there were remained in the samples

for much the same time as in 1952. Again, the 2 mm group did not begin to grow until the large specimens had disappeared from the samples. As in 1952, large specimens were absent in June, July and August, but unlike 1952 a secondary release of young took place in July. This followed maturation during April, May and June of specimens released in the winter. Growth continued over August and September

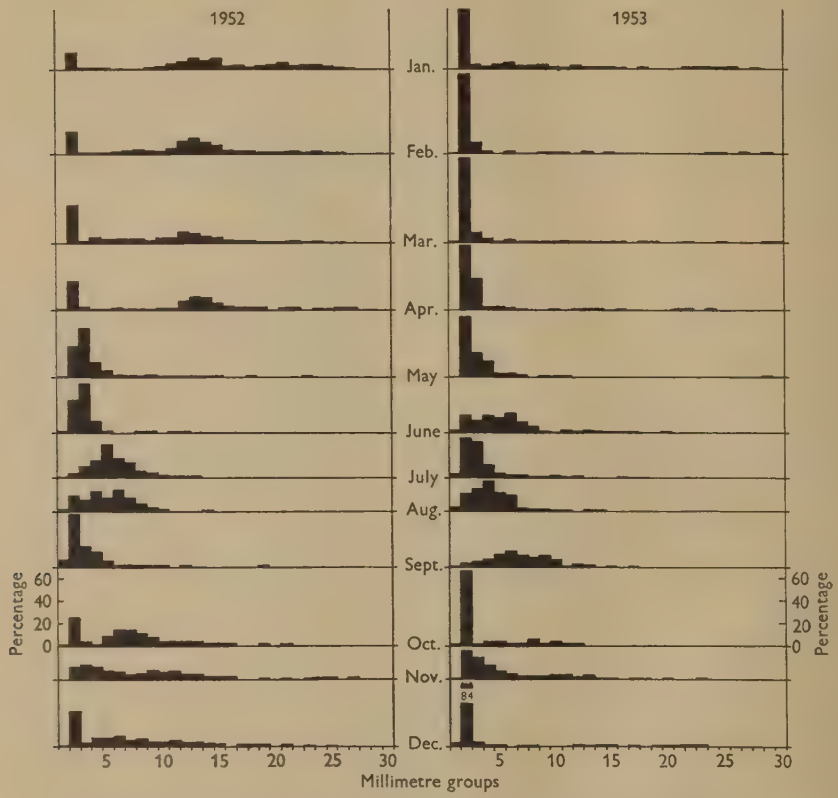

Fig. 6. Percentage frequency of *I. emarginata* in each millimetre size group.

and no further release of juveniles took place until October. In November, as in the previous year, the percentage in the 2 mm group decreased, and the total size-range in the sample had increased to that of the previous winter. Finally the release of juveniles began again in December.

Briefly then, there occurred during each winter a population of large males and females, which died off in spring, and a number of juveniles which began to grow in spring. Mass release of young, followed by growth, took place in April and September–October 1952, and April–May, July, and October 1953.

Fig. 8 shows the mean lengths of males, females and juveniles in each monthly sample, and the monthly mean sea temperatures for the locality from which the *Idotea* samples were taken. From January to April, when sea temperatures were lowest, the

mean size of both male and female *I. emarginata* were at their highest values. The mean size of juveniles showed no increase during these months. From April to June or July the mean sizes of both males and females dropped sharply as the larger specimens disappeared from the samples. At the same time, release of young ceased and growth of juveniles took place. From July onwards the mean length of males and females increased to the high value of the wintering population. The mean size of the juveniles followed a less regular pattern, but marked falls in mean length usually indicated times when mass release of young took place, and marked rises indicated a maturing stock of juveniles.

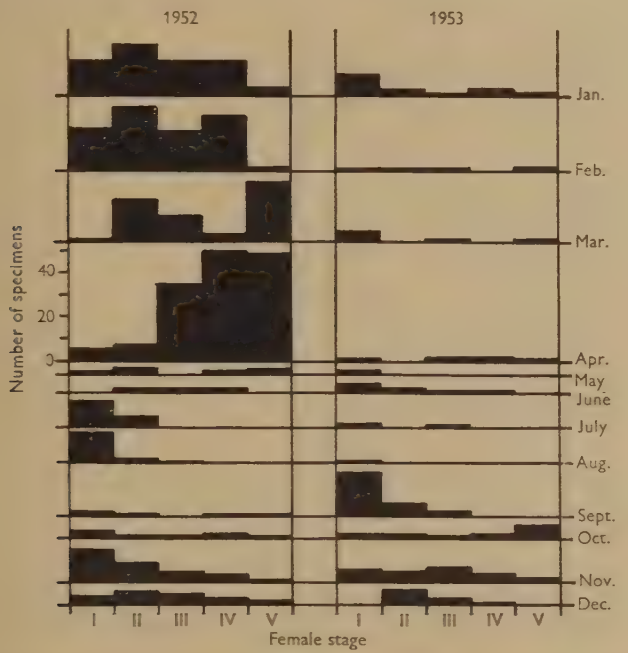

Fig. 7. Total females with embryos in each developmental stage, for each monthly subsample in 1952 and 1953. (I, females without brood pouch; II, females with brood pouch containing spherical eggs; III, females with elongated embryos; IV, females with embryos having appendages; V, females with empty brood pouch.)

DISCUSSION

Howes (1939) and Kjennerud (1950) divide the growth of *I. viridis* and *I. neglecta*, respectively, into clear-cut instars. In the present investigation it was shown (p. 273) that in *I. emarginata* only the first three instars after release can be recognized, and that beyond this it proved impossible to separate the stages. All specimens of *I. emarginata* taken in 1952 were divided into groups depending on the number of aesthetascs on their antennules. Specimens in which the aesthetasc complement of each antennule differed by more than one were not included; such specimens were rare and had probably lost aesthetascs through breakage. Fig. 4 shows the total number, the mean length, and the size range of all *I. emarginata* in each aesthetasc

group. No groups which can be regarded as instars can be extracted in the manner suggested by Howes, that is, by grouping together all those subsidiary groups which completely overlap in size range. The degree of overlapping is such that it is impossible to place any one individual into a particular growth stage.

Observations on Manx specimens of *I. viridis* and *I. neglecta* also seem to show more variation than is allowed for by Howes and Kjennerud in these two species. Growth

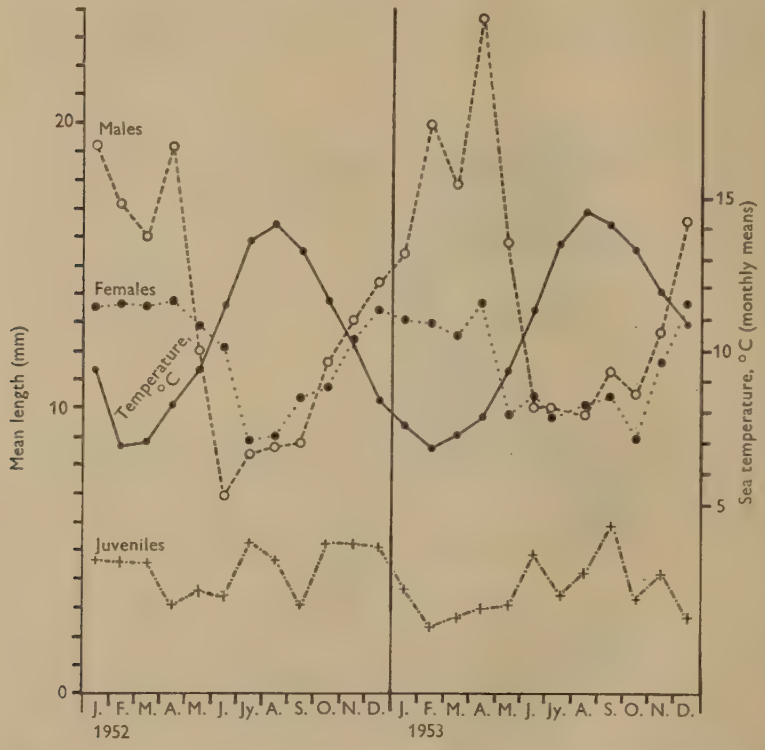

Fig. 8. The mean sizes of males, females and juveniles in monthly samples throughout 1952 and 1953, together with mean monthly sea temperatures for Port Erin Bay.

may differ in specimens of the same species from different localities, but it is worth noting that 18 out of 37 specimens of Manx *I. neglecta* failed to fit into any of the instars described by Kjennerud for that species. There are, then, limitations to the general application of the methods described by Howes and Kjennerud, and the use of these methods in taxonomy as a possible aid to recognizing not only species, but instars within a species, seems unjustified (Naylor 1955*b*). What is more, the intrinsic value of dividing the growth of *Idotea* into instars, each with its characteristic size-range, is subject to some limitations in *I. emarginata*. First, it has been demonstrated that juveniles released in spring are larger than those released in September, and this may apply to subsequent moulting stages in each case. Secondly, Fig. 4 shows that the older females are smaller than males in corresponding aesthetasc

groups, that is, in the corresponding moulting stage. These observations would seem to limit the value of generalizations about the size-range of moulting stages in *I. emarginata*.

Population changes in *I. neglecta* in Norway (Kjennerud 1950) differ markedly from those described here for *I. emarginata*. Whereas juvenile *I. emarginata* were found at most times of the year, the release of young by *I. neglecta* occurred only between April and July. Because of the restricted breeding season of *I. neglecta* Kjennerud was able to calculate its growth-rate and estimate its length of life. Attempts to calculate the growth-rate of *I. emarginata* were only partially successful, but it seems that *I. emaginata* live for a rather shorter time than the twelve months estimated for *I. neglecta*.

Seasonal changes in the population of *I. viridis* (Howes 1939) agree closely with those of *I. emarginata*, but even in *I. viridis*, the occurrence of the smallest specimens was restricted to May–August, and December.

ACKNOWLEDGEMENTS

My thanks are due to Mr J. S. Colman and Mr A. B. Bowers for helpful criticism of the manuscript.

SUMMARY

1. A large breeding population of *Idotea emarginata* is described, and an account of development, growth and reproduction is given.

2. In the adult brood-pouch the embryo passes through four distinct stages, and the embryos in the brood-pouch of any one female are all at the same stage of development.

3. The characteristics of the first three free-living stages are described, but beyond this it proved impossible to separate the stages. The growth of the antennule, antenna and telson, and the appearance of adult sexual characters, are described.

4. There is an overwintering population of large males and females, which die off in spring, and of juveniles which do not begin to grow until spring. Mass release of young, which immediately began to grow, took place in April and September–October 1952, and April–May, July, and October 1953.

5. These observations are discussed in relation to other species of *Idotea*.

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THE FOOD OF TITMICE IN OAK WOODLAND

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(With 4 Figures in the Text)

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INTRODUCTION

The following study was undertaken as part of the general investigation into population problems, and especially those of the great and blue tits (*Parus major* L. and *P. caeruleus* L.), which is being carried out at the Edward Grey Institute, Oxford, under the Director, Dr David Lack. The particular problem studied was the possible competition for food between these two species in an area of oak woodland, and their relationships with the other two species of titmice found in this habitat, the coal and marsh tits (*P. ater* L. and *P. palustris* L.). Moreover, it was hoped to compare the food of the birds with the available insect populations concerned, and to study predator-prey relationships.

According to Gause (1934), when closely related species occur in one habitat they are separated ecologically, or else one species, being better adapted for occupying the habitat, supplants the other. From field observations, Gause's principle has already been found to hold for a variety of birds (Lack 1944, 1947), and the genus *Parus* forms

a convenient group in which the application of this principle may be investigated in detail. In oak woods we find the great and blue tits nesting in similar positions, and moving in mixed flocks in the winter, so that according to Gause's hypothesis they should be separated by a difference in feeding habits. The proof of this difference in diet is presented in this paper.

Studies on the food of titmice have been made by Palmgren (1932) in Finland, on the northern willow tit, and in Holland the problem is being studied by Tinbergen (1949) and fellow workers. Kluijver (1950) has made some observations on the food brought to nestling great tits in pine woods in Holland, but did not correlate them with the insect population.

Previously, many workers on the food of birds have studied very large numbers of crop or gizzard contents, collected over large areas, and have drawn conclusions regarding the economic importance of the species which are unjustified by the data they present. This aspect of early food studies has been dealt with by Hartley (1948).

The method of recording individual birds seen feeding, used by Hartley (1953) and Gibb (1954*a*), can yield valuable information regarding feeding biology, and has the advantage that it does not interfere with the population, but it should be supplementary to a more detailed study of the actual food taken, as the records of a bird feeding in one particular place may have little bearing on the main food of the bird at that time. This was clearly demonstrated by the birds examined in December 1950, when several were followed through oak woodland, hunting in oaks for some time (in two cases for over half an hour), but when the food in their gizzards was analysed it was found to consist almost entirely of beechmast. The observational method has the additional disadvantages that if the food taken is small, it is impossible to determine visually what it is, and it can never solve the problem of whether the bird pecking at a bud is eating the plant tissue, or hunting for an insect concealed within it.

During a preliminary study in a mixed wood at Wytham, near Oxford, it was found that the variety of foods available and taken by the tits, was so great that any quantitative work, or comparisons of diet between species on a basis of gizzard analysis, was impossible, and for this reason the Forest of Dean, in west Gloucestershire, was chosen as a suitable area for this investigation. It is one of the few extensive areas of almost pure oak wood in England, which, although planted, approaches natural oak woodland. It was hoped that here, the uniformity of the habitat would simplify the correlation between the birds' diet and the insect population. This area had the additional advantage that it was so large that the necessary collection of titmice did not significantly deplete the population, and particular care was taken not to disturb the breeding population being studied. It must be stressed that the results of this work apply to the birds studied in this one area of oak woodland, during the period November 1948 to July 1951. Only a long-term investigation covering at least ten years will begin to eliminate the numerous variable factors, and give a more complete picture of the complex factors governing the relation of the birds to their food supply.

The main collecting region for sample material covered an area of some 350 acres in Barnhill Plantation and the adjoining north-eastern portion of Nagshead Plantation in the Forest of Dean (Fig. 1). The land lies between 200 and 600 ft above sea-level, and forms the western side of a valley which runs north to south, containing a stream,

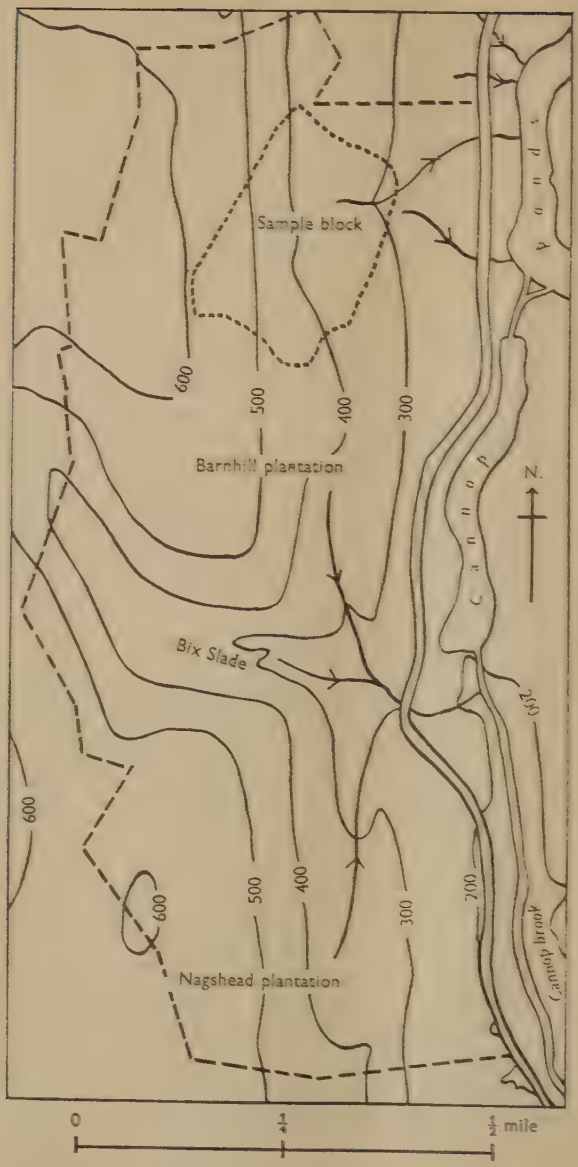

Fig. 1. The study area in the Forest of Dean, Gloucestershire. Contours in feet above sea-level.

Cannop Brook, and two pools, Cannop Ponds. It lies on the Forest of Dean Coal Measure, and the soil is consequently poor and acid, with a restricted ground flora. The oaks were planted, and are about 170 trees to the acre and about 150 years old (Taylor 1944). Thinning operations have reduced the density of the trees, and in a

sample block of 12 acres in the middle of Barnhill Plantation a total count in 1951 showed the density to be 31 oaks per acre. The general habitat most nearly approaches that of Tansley's Quercetum sessiflorae on moderately acid soils (Tansley 1939), the field layer being largely a *Pteridium-Holcus-Scilla* society, with other grasses and some smaller plants. The oaks are mostly the pedunculate species (*Quercus robur* L.) but the sessile oak (*Q. petraea* Liebl.) and hybrid forms are also common. Table 1 shows the distribution of trees in the sample block of 12 acres in Barnhill Plantation. The

Table 1. *Trees and shrubs in Barnhill Plantation, 1951*

Numbers per acre, tree layer > 20 ft high, shrub layer > 1 and < 20 ft.

	Tree layer	Shrub layer
Oak (*Quercus robur* L.), (*Q. petraea* Liebl.)	31	15*
Birch (*Betula pendula* Roth.)	9*	6*
Sweet chestnut (*Castanea sativa* Mill.)	5	11*
Sycamore (*Acer pseudo-platanus* L.)	1	0·4
Hawthorn (*Crataegus oxycanthoides* Thuill.)	0·7	2
Holly (*Ilex aquifolium* L.)	0·4	4*
Ash (*Fraxinus excelsior* L.)	0·2	0
Hazel (*Corylus avellana* L.)	0	1
Douglas fir (*Pseudotsuga taxifolia* Britt.)	0	0·2
Crab apple (*Malus pumila* Mill.)	0	0·1
Rowan (*Sorbus aucuparia* L.)	0	0·2

* Local clumps.

sample block is typical of the open sheep-grazed areas of oak woodland, and is representative of the slopes of Nagshead and Barnhill Plantations where the bird samples were collected. The effect of grazing is to reduce, and in places to eliminate, the shrub layer, and only on the steepest parts of the slopes is this layer found, where it is formed of young holly and sweet chestnut. Birch trees are found mainly on the spoilheaps of an old mine, while ash is restricted to the edges of a small stream flowing through the area. Ivy (*Hedera helix* L.) was common on many of the oaks, but was cut when the plantation was thinned in 1950.

A deep valley, Bix Slade, cuts into the hillside, dividing the two plantations, and has a stream running along it. Here are found well-grown beeches (*Fagus sylvatica* L.), many birches, willows (*Salix caprea* L.) and clumps of blackthorn (*Prunus spinosa* L.). The road running along the bottom of the plantations from the Coleford–Speech House road to Parkend, forms a boundary to the collecting area, and on the Cannop Pools side is edged by alders (*Alnus glutinosa* (L.)).

The field layer too shows the effect of grazing; brambles for example are absent, and the number of plants reduced. It is composed largely of bracken (*Pteridium aquilinum* (L.)), bluebell (*Scilla non-scripta* (L.)), and the grass *Holcus mollis* L. Also common are wood sorrel (*Oxalis acetosella* L.), and in patches, foxglove (*Digitalis purpurea* L.) and violet (*Viola canina* L.). The grass *Deschampsia flexuosa* (L.) and stitchworts (*Stellaria* spp.) are fairly common, while in the rides *Veronica* spp., *Potentilla erecta* (L.), and *Lysimachia nemorum* L. are found. In damp places *Juncus effusus* L. and *Luzula* spp. occur, with occasional ferns. The ground flora varies with the degree of slope in the plantation, bluebells being uncommon on the steeper upper

part of the hillside, and the rides often provide a habitat suitable for a greater variety of plants than the more shady woodland. Mosses are also frequent, the commonest being *Polytrichum formosum* Hedw., *Thuidium tamariscinum* (Hedw.) and *Hypnum cupressiforme* Hedw. This latter species is also common on the tree trunks, while *Dicranoweisia cirrata* Lindb. is found on the larger horizontal boughs of the oaks. From the point of view of the importance of the plants in the area to the birds, the species concerned are wood sorrel and violet whose seeds are eaten, and the moss *Dicranoweisia* where the sporogonia are taken.

GIZZARD ANALYSES

(*a*) *Technique*

The alimentary tract was placed in 70% alcohol immediately after collection as deterioration is rapid (van Koersveld 1951), and later the gizzard contents were washed out with alcohol and sorted under a binocular microscope. Adult insects were counted by the number of heads, or distinct portions of the head, together with the wings and genitalia when present. Eggs were listed separately only when taken after laying, as distinct from any present in the female insect. Larvae were counted by heads, or fragments of heads, but when these were too soft to be preserved, a length of body measuring over half the total length and bearing some characteristic feature such as the crotchets of lepidopterous larvae, was taken to equal one larva. Spiders were counted by the number of chelicerae present. It has been argued that the harder parts of insects and spiders may be retained in the gizzard (Palmgren 1932), but in many cases it was possible to correlate their presence with that of other softer portions, and it was felt that they offered the only constant criterion of numbers. As the same techniques were used throughout the investigation it is possible to make valid comparisons between the four species of birds.

Seeds were counted and listed numerically, any fragment over half being taken as one seed. For other vegetable material such as nut, gall and bud tissue, an estimate of the percentage of the total volume of the gizzard contents was made, as no other measurement was feasible. Gravimetric and detailed volumetric methods were discarded as the bulk of the material was too small for these methods to be used successfully. The average volumes of total gizzard contents of the four Paridae in this investigation were: great tit 1·0 ml, blue tit 0·5 ml, coal and marsh tit 0·4 ml.

Table 2. *Sample numbers of birds*

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Total
Great tit	11	15	12	13	2	13	25	19	11	6	11	12	150
Blue tit	25	25	26	15	17	22	34	17	21	13	16	22	253
Coal tit	5	6	13	4	2	2	0	5	2	8	6	7	60
Marsh tit	4	2	4	4	0	4	0	2	6	3	5	4	38

In the following tables the percentages and occurrences are based on the sample numbers of birds shown in Table 2. Sample numbers are small, but the general agreement between individuals was found to be such that in this uniform habitat they are thought to be adequate, at least in the case of the two typical oak wood species,

the great and blue tits. For convenience, and with some entomological justification, the months may be divided into four seasons, November, December, January being winter; February, March, April, spring; May, June, July, summer; and August, September, October, autumn. In this paper references to the seasons are based on this division, and the bird samples were collected over a period of three winters, and two springs, summers and autumns.

(*b*) *Insect food*

For the comparison of the diets of the four species of titmice only the main insect groups have been included, and in the following tables, showing the percentage occurrence of insects, only those groups with an occurrence of over 5% of the total insects in one species of bird in any one month have been tabulated. In groups where the immature forms have different habitats from the adults, or where the adults are sessile, or are gregarious, these have been tabulated separately.

The present tense is used to indicate that a particular group or species occurred in more than one year (and is probably therefore a general feature of the diet in the month concerned), while the past tense is used to indicate that the animals occurred in one year only, and may be exceptional. The nomenclature is in accordance with *A Check List of British Insects* (Kloet & Hincks 1945). A complete list of all the insects taken by the titmice will be published shortly (Betts, in press). The original data are deposited in the Edward Grey Institute, Oxford.

NOVEMBER

Table 3. *Percentage composition of insects in the diet of titmice in November*

	Great	Blue	Coal	Marsh
Total insects in sample ...	151	1527	211	13
Hemiptera-Heteroptera	6	—	6	—
Hemiptera, Coccidae	—	39	—	8
Lepidoptera imagines	12	—	—	92
Lepidoptera pupae	6	23	5	—
Lepidoptera larvae	14	17	13	—
Lepidoptera eggs	10	—	42	—
Coleoptera imagines	20	—	—	—
Hymenoptera imagines	—	—	10	—
Hymenoptera larvae	16	—	7	—
Other insects	16	21	17	0

HEMIPTERA. In the great tit these are mainly pentatomids (especially *Troilus luridus* Fabr.), and *Nabis* spp., while in the coal tit the nymphs (generally third instar) of the pentatomid *Pentatoma rufipes* (L.) occur. The coccids are represented by six species, but in both blue and marsh tits *Asterolecanium variolosum* (Ratz.) is by far the most common, but shows a decrease in 1950, with an increase in the scale *Aspidiotus zonatus* Fr.

LEPIDOPTERA. The moths taken are those of the winter moth *Operophtera brumata* (L.), and the umber moths *Erannis aurantiaria* (Esper) and *E. defoliaria* (Clerk), while the pupae are those of the leaf-mining gracilarid *Lithocolletis* sp. The larvae are

of this species, together with another leaf-miner *Tischeria complanella* (Hueb.), and coleophorids, especially *Coleophora lutipennella* (Zell.). The leaf-miners were more abundant in 1950 and averaged 38 per blue tit, occurring in 92 % of the sample. The eggs of the vapourer moth (*Orgyia antiqua* (L.)) were found in one great tit, and those of *Colotois pennaria* (L.) in one coal tit.

Coleoptera. The coccinellid *Adalia decempunctata* (L.) and the weevil *Strophosomus melanogrammus* (Forst.) are the main beetles taken in this month.

Hymenoptera. The adults are small ichneumonids and Cynipidae, and the larvae those of the latter family, especially the galls of *Andricus ostreus* (Hart.) in 1949, and *A. collaris* (Hart.) in 1950.

DECEMBER

Table 4. *Percentage composition of insects in the diet of titmice in December*

	Great	Blue	Coal	Marsh
Total insects in sample ...	650	1899	241	114
Psocoptera	—	6	—	—
Hemiptera-Heteroptera	—	—	8	—
Hemiptera, Coccidae	—	25	25	58
Hemiptera eggs	—	—	16	—
Lepidoptera imagines	52	23	24	35
Lepidoptera pupae	—	7	6	—
Lepidoptera larvae	—	12	—	—
Lepidoptera eggs	26	—	—	—
Coleoptera larvae	—	6	—	—
Hymenoptera larvae	9	—	—	—
Diptera larvae	—	8	—	—
Other insects	14	12	21	7

Psocoptera. In 1948 two blue tits were found with the nymphal forms, and a few adults, of an unidentified psocid, over a hundred being present in one bird.

Hemiptera. The coal tit again takes the nymph of *Pentatoma rufipes* and one bird in 1950 contained aphid eggs. The coccids are mostly *Asterolecanium variolosum* in all three species.

Lepidoptera. The adult winter moth with some mottled umbers are again taken in this month. In 1949 the total samples of all three species (no marsh tits were obtained) contained winter moths, with an average of 43, 28, 30, per great, blue and coal tit respectively. The pupae in the blue and coal tits are those of *Lithocolletis* sp., and the larvae mostly *Coleophora lutipennella*. The eggs taken by two great tits in 1950 were those of *Orgyia antiqua*, and in 1949 one bird had eaten eggs of *Ennomos quercinaria* (Hufn.).

Coleoptera. The blue tit takes larvae of a number of species but those of *Dasytes* sp. and the cerambycid *Leiopus nebulosus* (L.) are the most important.

Hymenoptera. Cynipid larvae, especially *Andricus ostreus* in 1949, are eaten by the great tit.

Diptera. Two blue tits in 1948 contained unidentified small muscid larvae.

JANUARY

Table 5. *Percentage composition of insects in the diet of titmice in January*

	Great	Blue	Coal	Marsh
Total insects in sample ...	197	2853	793	326
Collembola	—	—	—	65
Hemiptera-Heteroptera	5	—	8	—
Hemiptera-Homoptera	—	—	16	—
Hemiptera, Coccidae	—	34	50	16
Lepidoptera imagines	7	—	—	—
Lepidoptera larvae	—	24	—	—
Lepidoptera eggs	20	—	—	—
Coleoptera imagines	45	—	—	—
Coleoptera larvae	—	16	—	—
Hymenoptera larvae	—	—	6	—
Diptera larvae	—	10	—	—
Other insects	23	16	20	19

COLLEMBOLA. In 1949 one marsh tit contained 211 unidentified Collembola.

HEMIPTERA. As in November the great tit takes mainly pentatomids, *Elasmucha grisea* (L.) and *Acanthosoma haemorrhoidale* (L.), and lygaeids, *Drymus* spp., while the coal tit continues with *Pentatoma rufipes* nymphs. In this month, too, half the coal tits contain Chermidae, *Chermes melanoneura* (Foer.) and *Trioza remota* Foer., and scale insects are again important for all species except the great tit. The same species of coccids occur as previously, together with the immature females of *Eulecanium coryli* (L.).

LEPIDOPTERA. These are adults of *Erannis* spp. and mostly *E. leucophaearia* (Schiff.). The larvae found in blue tits are coleophorids, and these and *Lithocolletis* sp. occur in the coal tit. Eggs are again those of *Orgyia antiqua*.

COLEOPTERA. The adult beetles are represented by the weevil *Strophosomus melanogrammus*, one great tit containing the remains of 20 individuals, and an average of 9 per bird. The larvae eaten by the blue tit are of several families—Dasytidae, Pythidae, Mordellidae and ?Chrysomelidae—all having one feature in common, that they occur under bark and in moss, etc.

HYMENOPTERA. The coal tit continues to take cynipid larvae but 1950 was the peak with *Andricus ostreus*.

DIPTERA. Larval sciarids and cecidomyids occur in the blue tit.

FEBRUARY

Table 6. *Percentage composition of insects in the diet of titmice in February*

	Great	Blue	Coal	Marsh
Total insects in sample ...	712	2732	1246	159
Hemiptera, Coccidae	—	31	80	42
Lepidoptera imagines	—	—	—	9
Lepidoptera larvae	—	7	—	12
Coleoptera imagines	18	—	—	—
Coleoptera larvae	—	18	—	—
Hymenoptera imagines	30	6	—	32
Diptera imagines	34	—	—	—
Diptera larvae	—	36	13	—
Other insects	18	3	7	4

HEMIPTERA. In the blue and marsh tit the usual scales occur with an increase in the proportions of *Aspidiotus zonatus* and *Lepidosaphes ulmi* (L.) in 1950, although *Asterolecanium variolosum* is still the commonest. The coal tit, however, in the one year when a sample was obtained, 1950, had fed almost entirely on the ash scale *Fonscolombia fraxini* (Kalt.), averaging 141 scales per bird and 100% occurrence. Although ash trees were not common (0·2 per acre in the sample block of 12 acres) the insect occurs in such large numbers that one tree could provide food for many birds. The insect plus felt-like sac is taken, which shows that the widely held belief that they are distasteful to birds is not correct (Newstead 1900–03). Gibb (1954*a*) and Hartley (1953) have also recorded the preference of coal tits for ash trees in spring in other localities in mixed woodland, so that it does not appear to be a localized habit.

LEPIDOPTERA. The moths were *Erannis leucophaearia*, and were found in both marsh tits in 1950. The larvae are again coleophorids, mostly *Coleophora lutipennella* in the blue tit.

COLEOPTERA. In 1949 these were mainly the weevil *Strophosomus melanogrammus*, but in 1950 the coccinellid *Adalia decempunctata* becomes more frequent. The larvae taken by the blue tit are mostly of the species ?*Orsodacne lineola* (Panz.), together with some of the species recorded in the last month.

HYMENOPTERA. The great tit takes a large number of the adult gall-wasp *Neuroterus lenticularis* (Oliv.), which emerges from the litter in this month and goes to the oak buds to oviposit. They are also found in the blue tit, and have 100% occurrence in the great tit, 87% in the blue tit, averaging 15 and 9 per bird respectively. Three of the four marsh tits in the sample contain this insect, averaging 14 per bird.

DIPTERA. The great tit takes adult *Sciara* sp., which in 1950 averaged 39 per bird, and 83% occurrence. In the blue tit Diptera are represented by cecidomyid larvae, and one coal tit in 1950 had 154 sciarid larvae.

MARCH

Table 7. *Percentage composition of insects in the diet of titmice in March*

	Great	Blue	Coal
Total insects in sample ...	58	475	154
Collembola	—	9	—
Hemiptera-Heteroptera	5	—	—
Hemiptera, Coccidae	—	45	36
Lepidoptera larvae	7	17	10
Coleoptera imagines	35	7	14
Hymenoptera imagines	26	16	36
Hymenoptera pupae	10	—	—
Diptera pupae	9	—	—
Other insects	8	6	4

COLLEMBOLA. In 1950 one blue tit contained 41 Collembola of the species *Mydonis nivalis* (L.).

HEMIPTERA. Nabids and the pentatomid *Acanthosoma haemorrhoidale* occurred in one great tit. The female *Eulecanium coryli* is the most abundant scale in both the blue and coal tits in this month.

LEPIDOPTERA. The larvae are still coleophorids in the blue and coal tits, with

Coleophora lutipennella common in the blue tit. A few tortricoid larvae occur in the latter species, while the great tit contained tinaeoid larvae and one geometer.

COLEOPTERA. Curculionids, with *Strophosomus melanogrammus* by far the most common, occurred in the great tit. Weevils are also the most common beetles in the other two tit species, but are of different genera, being those of *Coeliodes* spp.

HYMENOPTERA. All three species of titmice contain adult cynipids, especially *Andricus* sp. and *Neuroterus* sp. Both great tits had taken unidentified pupal cocoons.

DIPTERA. Five unidentified schizophoran pupae were present in the great tits.

APRIL

Table 8. *Percentage composition of insects in the diet of titmice in April*

	Great	Blue	Coal	Marsh
Total insects in sample ...	360	2824	219	190
Hemiptera, Coccidae	—	6	57	7
Lepidoptera larvae	—	—	10	—
Coleoptera imagines	24	—	5	14
Hymenoptera imagines	11	17	26	77
Diptera imagines	57	—	—	—
Diptera larvae	—	71	—	—
Other insects	8	6	3	2

HEMIPTERA. The scale *Eulecanium coryli* is still the most commonly occurring species in the blue tit, but the ash scale also occurred in over a third of the birds in 1950, and is the commonest scale in the coal tit. Its absence in the preceding month in the coal tit is probably due to the lack of sample material in this year, and not to a change in diet.

LEPIDOPTERA. The coleophorid larvae are still found in the blue and coal tits, but only in the latter do they form an appreciable part of the insect food.

COLEOPTERA. The adult beetles taken by the great tit are mostly weevils, with *Strophosomus melanogrammus* still the most frequent and *Coeliodes* spp. also common. The silphid *Xylodrepa quadripunctata* (L.) became more numerous in 1950, and in 1949 elaterids, especially *Agriotes pallidulus* (Ill.) were found to be common. In the coal tit *Coeliodes* spp. occur, and these species together with *Strophosomus melanogrammus* are found in the marsh tit.

HYMENOPTERA. All four species of titmice take adult cynipids, which in this month in both years are those of *Neuroterus aprilinus* (Gir.), the April bud gall-wasp.

DIPTERA. The great tit contains relatively large numbers of bibionid flies, *Bibio varipes* Meig. and *B. reticulatus* Loew being the two species in 1949 and 1950. There is 100% occurrence with an average of 15 per bird. The larval forms in the blue tit are cecidomyids *?Contarinia* sp. from oak buds, and these larvae in 1950 averaged 200 per bird and 91% occurrence.

MAY

Table 9. *Percentage composition of insects in the diet of titmice in May*

	Great	Blue
Total insects in sample ...	733	414
Hemiptera, Coccidae	—	21
Lepidoptera pupa	—	20
Lepidoptera larva	84	56
Coleoptera imago	7	—
Other insects	9	3

In this month only great and blue tits were available as the young were taken from nest-boxes. One brood of great tits and one adult were obtained in 1949, and one complete brood with one adult, together with some young from another brood, in 1950. Two broods of blue tits and three adults were obtained in 1949, and one brood with one adult in 1950. The young were on average about three-quarters grown. As there was little difference in the foods and quantities of insects present in the adults and nestlings it was decided to group them together.

HEMIPTERA. In 1950 only, 93% of the blue tits contained the fully developed brown scale *Eulecanium coryli*. In 1949 this insect was not common in the habitat and this factor may govern its occurrence in the food, for in 1951 it was again common in May and was fed in large numbers to a brood of great tits for a short period of time (see p. 310). It is surprising that under these circumstances it does not occur in the great tit samples, but it may well be that the young were too advanced for such small items to be brought to the nest, for in the observed brood in 1951 scales were not brought after the young were 11 days old.

LEPIDOPTERA. Of the pupae present few could be identified to specific rank, but *Cacoecia* sp. were common, and all the pupae were Tortricoidea. Due to a difference in seasons pupation was earlier in 1950, and it is only in this year that pupae are found in any numbers in the May samples. The larvae are mostly beyond identification, but geometers form the major part of those which were represented by identifiable remains, and of these the larvae of the winter moth (*Operophtera brumata*) are the commonest, together with *Erannis* spp. and some Caradrinidae, especially *Orthosia cruda* (Schiff.) and *Cosmia trapezina* (L.).

COLEOPTERA. The silphid *Xylodrepa quadripunctata* and the elaterid *Athous haemorrhoidalis* (Fabr.) are the common beetles found in the great tit in both years, and both of these species were fed to young birds in 1951 forming 10% of the diet of the observed brood, a figure which is slightly larger than that found in the sample birds.

JUNE

Table 10. *Percentage composition of insects in the diet of titmice in June*

	Great	Blue	Coal	Marsh
Total insects in sample ...	799	725	218	63
Hemiptera, Coccidae	—	7	6	14
Hemiptera, Aphididae	53	59	66	—
Lepidoptera pupae	—	13	6	13
Lepidoptera larvae	6	—	—	—
Coleoptera imagines	22	6	12	43
Hymenoptera pupae	—	—	—	9
Diptera larvae	—	—	—	9
Other insects	19	15	10	11

HEMIPTERA. The scales are *Eulecanium coryli*, but the numbers occurring are small, while the oak aphis *Vacuna dryophila* (Schr.) was the dominant insect in 1949 in all species of titmice sampled (there were no marsh tits in the 1949 sample). The aphis did not occur in any of the birds in 1950, when it was not common, but in 1949, 64 and 50% of the great and blue tits contained this insect. It has a patchy distribution,

being wingless, and is found in large numbers only on the leaves of some trees, which may explain the low frequency of occurrence and large numbers found in the bird samples.

LEPIDOPTERA. The pupae in all species are tortricoids, while in the great tit the larvae are mostly Caradrinidae and unidentified species.

COLEOPTERA. Adult beetles in the great tit are represented by elaterids of the genus *Athous*, with *A. haemorrhoidalis* the most common; and the weevils *Phyllobius* spp., more especially *P. argentatus* (L.) and *P. maculicornis* Germ. These weevils are also found in the other titmice but not the elaterids. In the blue tit the coccinellid *Adalia decempunctata* occurred in 1950, while the first of the nut-weevils *Curculio* spp. appear.

HYMENOPTERA. Unidentified pupal cocoons are found in the marsh tit and in the other titmice too, but not in any numbers.

DIPTERA. Muscid larvae occurred in the marsh tit.

JULY

Table 11. *Percentage composition of insects in the diet of titmice in July*

	Great	Blue	Coal	Marsh
Total insects in sample ...	272	624	48	104
Hemiptera-Homoptera	21	—	6	6
Hemiptera, Coccidae	12	9	44	6
Hemiptera, Aphididae	—	18	—	—
Hemiptera eggs	—	18	—	—
Neuroptera larvae	—	6	—	—
Lepidoptera imagines	—	—	10	8
Coleoptera imagines	35	21	27	61
Hymenoptera imagines	18	10	—	6
Other insects	14	19	12	13

HEMIPTERA. The jassids *Aphrodes* spp., especially *A. bicinctus* (Schr.), are the main homopterans in the great tit, while the coal and marsh tits took the bythoscopid *Bythoscopus lanio* (L.) in 1950, with one coal tit containing a nymph and adult of *Ledra aurita* (L.). The coccids are still *Eulecanium coryli* and by this time they are merely egg-sacs or parasitized. Aphids were found only in the blue tit in 1949, and are another oak species *Myzocallis annulatus* (Hart.); again the 50% occurrence indicates a patchy distribution. The eggs are Pentatomidae.

NEUROPTERA. The larvae of *Hemerobius* sp. and *Chrysopa ciliata* Wesm. occur in some numbers in the blue tit, and a few in the coal tit, in 1949.

LEPIDOPTERA. Adult tortricoids are taken by all four species, but only form an appreciable part of the diet of the coal tit. Two great tits in 1949 contained the adult large yellow underwing (*Triphaena pronuba* (L.)).

COLEOPTERA. In the great tit in both years the weevil *Strophosomus melanogrammus* is the most numerous beetle, and this is found in the other titmice with the exception of the blue tit, which feeds more on the cocinellid *Adalia decempunctata*. The nut weevil *Curculio venosus* (Grav.) is also common in all except the great tit, and the marsh tit contains, in addition, some *Phyllobius* spp.

HYMENOPTERA. In 1950 one great tit contained 16 workers of the hive bee *Apis*

mellifera L. and one large *Bombus* sp., otherwise the adults are mostly ichneumonoids. No fragments of the stings were found and presumably these were removed by hammering before the bees were eaten. In the blue and marsh tits, and in smaller numbers in the coal tit, adult ichneumonoids are found. The blue tit also contain some cynipids, and in 1949 three birds had eaten 15 *Synergus* sp.

AUGUST

Table 12. *Percentage composition of insects in the diet of titmice in August*

	Great	Blue	Coal	Marsh
Total insects in sample ...	89	166	144	38
Hemiptera-Heteroptera	7	—	10	—
Hemiptera-Homoptera	30	22	14	16
Hemiptera, Coccidae	—	7	7	5
Hemiptera, Aphididae	—	—	10	—
Hemiptera eggs	—	—	8	—
Neuroptera larvae	—	—	—	5
Lepidoptera imagines	6	5	—	5
Lepidoptera larvae	—	—	—	21
Coleoptera imagines	16	16	12	27
Coleoptera larvae	—	7	—	—
Hymenoptera imagines	33	19	27	5
Hymenoptera larvae	—	7	—	—
Diptera larvae	—	—	—	13
Other insects	9	17	11	2

Hemiptera. The pentatomid *Elasmucha grisea*, which is found on birch, occurs in coal tits in both years, together with pentatomid eggs (probably of the same species), and the adult was found in great tits in 1950. Of the Homoptera, *Bythoscopus lanio* nymphs and *Chermes* spp., especially *C. melanoneura*, are found in the blue tit, while the former species is common in both the coal and marsh tits. The scale *Eulecanium coryli* is still found, with some *Lepidosaphes ulmi*, in the blue tit, and the aphid *Myzocallis annulatus* in the coal tit.

Neuroptera. *Chrysopa* spp. larvae occurred in 1949 samples.

Lepidoptera. Small moths, Tortricoidea and Tinaeoidea, are found in all species, and in 1949 one great tit again contained the adult *Triphaena pronuba*. Of the larvae in the marsh tit most were unidentifiable, but one lymantrid *Dasychira pudibunda* (L.) could be recognized.

Coleoptera. The nut-weevil *Curculio venosus* is common in the blue and coal tits, and of the short-snouted weevils *Phyllobius* spp. and *Strophosomus melanogrammus* are the most frequent. Only the great tit contains elaterids, and in 1949 two birds contained three specimens of the rare weevil *Trachodes hispidus* (L.). The larvae are *Dasytes* sp.

Hymenoptera. Ichneumonids are found in all species, but in the great tit in association with wasps *Vespula* sp. (three in one bird in 1949), and the ants *Myrmica ruginodis* Nyl. and *Formica* sp. (six in two birds in 1950). In the blue tit, adult and larval cynipids are important, while the coal tit in this month in 1949 contained 15 *Synergus gallae-pomiformis* (Fonsc.) in four birds.

Diptera. One marsh tit had taken five muscid larvae.

SEPTEMBER

Table 13. *Percentage composition of insects in the diet of titmice in September*

	Great	Blue	Coal	Marsh
Total insects in sample ...	260	340	54	80
Insect indet. eggs	—	—	—	25
Hemiptera-Heteroptera	—	—	9	—
Hemiptera-Homoptera	10	—	—	—
Hemiptera, Coccidae	—	10	—	—
Lepidoptera larvae	24	19	22	51
Coleoptera imagines	45	5	26	10
Coleoptera larvae	—	12	—	—
Hymenoptera imagines	10	23	22	—
Hymenoptera larvae	—	11	11	—
Diptera larvae	—	5	—	—
Other insects	12	15	9	14

One marsh tit in 1950 contained 20 unidentified eggs, and four occurred in two blue tits in 1949.

HEMIPTERA. The pentatomid *Elasmucha grisea* and the lygaeid *Kleidocerys resedae* (Panz.) are found in the coal tit, while the homopteran *Megophthalmus scanicus* (Fall.) and *Aphrodes* spp. occur in the great tit. The scales are *Asterolecanium variolosum*, and are found only in the blue tit.

LEPIDOPTERA. In the great tit these are mainly lymantrid caterpillars, and three *Dasychira pudibunda* larvae were identified in one bird. One bird, however, in 1949, contained 34 *Coleophora* sp., a larva rarely taken by this species. In the other titmice the larvae are unidentified tortricoids, with coleophorids in the marsh tit, and large numbers of the leaf-mining larvae of *Lithocolletis* sp. and *Tischeria complanella* (Hueb.).

COLEOPTERA. The weevil *Strophosomus melanogrammus* is found in all four bird species; the great tit also contains other short-snouted weevils, namely *Otiorrhyncus singularis* (L.) and *Phyllobius* spp. The coccinellid *Adalia decempunctata* occurs in small numbers in all species. The larvae are taken by the blue tit only, with the exception of one cerambycid larva in a great tit, and are *Anaspis* sp. and *Dasytes* sp.

HYMENOPTERA. As in the previous month the adult Hymenoptera in the great tit are ichneumonoids and, in 1949, wasps *Vespula* spp. Four birds had taken 11 wasps of which five were males, three were workers and three of undetermined sex. In the blue tit, in 1950, six of the eight birds examined contained 65 males of the ant *Myrmica laevinodis* Nyl. Proctotrupid wasps, *Exallonyx* sp., occurred in two coal tits in 1950. Larval cynipids are found in the blue tit in some numbers, and are *Andricus ostreus* in 1949, and *A. collaris* (Hart.) in 1950.

DIPTERA. In 1949 cecidomyid and sciarid larvae occurred in two blue tits.

OCTOBER

Table 14. *Percentage composition of insects in the diet of titmice in October*

	Great	Blue	Coal	Marsh
Total insects in sample ...	186	896	447	157
Hemiptera, Coccidae	—	7	—	—
Hemiptera, Aphididae	—	—	38	80
Lepidoptera larvae	32	68	55	9
Lepidoptera eggs	8	—	—	—
Coleoptera imagines	37	—	—	—
Hymenoptera imagines	12	—	—	—
Hymenoptera larvae	—	9	—	8
Diptera larvae	—	5	—	—
Other insects	11	11	8	3

Hemiptera. The scales are mostly *Asterolecanium variolosum*, and the aphis found in the 1950 sample of coal and marsh tits the sycamore aphis (*Drepanosiphum platanoides* (Schr.)). Both marsh tits and one coal tit were near sycamores when taken, but, as with the ash, it is not a common tree (see Table 1), and although every effort was made to find birds in the general oak woodland, it was found that these two species were concentrating on the isolated sycamores or else feeding on beechmast. This preference for sycamore was not seen in the other titmice, and no aphids were found in them.

Lepidoptera. The caterpillar of the oecophorid *Diurnea fagella* (Schiff.) was very abundant in 1949, and in that year occurred in five of the six great tits, all the marsh tits, and half the blue and coal tits. In the great tit there was an average of seven larvae per bird, but the numbers were smaller in the other species, and less than one in the blue tit. The commonest larvae in both years in the blue, coal and marsh tits are the leaf-miners, *Tischeria complanella* and *Lithocolletis* sp. The eggs were those of *Orgyia antiqua* in 1950.

Coleoptera. These are the weevil *Strophosomus melanogrammus* in both years, and the coccinellid *Adalia decempunctata* in 1949.

Hymenoptera. Ichneumonids were found in the great tit in 1949, together with wasps *Vespula* sp. These occurred in five of the six birds in the sample, and of the nine wasps found at least seven were males as the genitalia were present. The larvae are cynipids as in the previous month.

Diptera. Cecidomyid and muscid larvae are found in the blue tit.

(*c*) *Miscellaneous animal foods*

Spiders. The fragmentary material, and the occurrence of immature forms, made it impossible to identify most of the spiders, and it was decided to count them with no attempt at identification. The group is widespread and occurs in relatively small numbers in the birds, so that the labour involved in identifying species from gizzard fragments was felt to be unjustified in this type of investigation. All four species of titmice take spiders throughout the year, but the average number per bird never exceeded nine in any one month. Comparing the spider-eating habits of the great and blue tits throughout the year, it will be seen from Table 15 that the two species

ave little in common, as the peak in occurrence, and in the average number of piders per bird (8·0), in the great tit comes in the early part of the year, whereas the lue tit shows a peak in both these features in August (average number 5·5 spiders er bird). The drop in percentage occurrence in June in the other three species is not nown by the blue tit, and this bird takes a more constant proportion of spiders idged by the numbers per bird. The coal tit in the winter and spring months has high average number of spiders (5·8 per bird), and these are found in nearly all the irds examined. The number of marsh tits is too small for valid comparison, but from he table it would appear that it takes fewer spiders than the other tits, while the coal t takes the most. The percentage of spiders in the diet fluctuates through the year, ut a marked increase occurs in the autumn months in all four species, corresponding ith the period of maximum abundance of spiders. Although no detailed identifi-ations were made, the great tit is most frequently found to contain large spiders of he families Lycosidae and Argyopidae, while the spiders taken by the blue tit are mall, and are mostly members of the families Theridiidae and Linyphiidae.

Table 15. *The percentage occurrence of spiders*

	Great tit	Blue tit	Coal tit	Marsh tit
November	91	92	100	50
December	87	92	100	50
January	92	89	92	100
February	100	80	100	75
March	100	53	100	—
April	92	82	100	100
May	96	82	—	—
June	47	88	80	50
July	91	86	100	67
August	83	100	75	100
September	100	88	83	100
October	75	77	91	50
Average number of spiders per bird	3·6	2·8	4·8	2·5

The egg cocoons of spiders, sometimes containing eggs but more often found as a angled mass of silk, are found fairly frequently, but, with two exceptions, never in ny number. In the May samples of great tits 24 of the 25 birds examined contain eggs nd cocoons of lycosid spiders, averaging 11 per bird, and as the female spider carries he cocoon, the average number of spiders is high also. One nest watched three days efore the young were taken, showed the adults to be feeding almost entirely on the round, where at the time lycosids were very abundant. As the same thing occurred in oth years, at a time when caterpillars were plentiful, it appears that the great tit xploited this temporary abundance of ground spiders. In other species of titmice he peak consumption of cocoons comes in June and July, but the numbers are small. one of the other species contain Lycosidae, and were rarely observed feeding on the round in May.

The consumption of spiders and their cocoons is general among the tits, but does ot form an important part of their diet. Spiders are such a numerous and widespread roup that it might be expected they would be more fully exploited as a source of

food. It is known from nest observations in this area in 1951 that the number of spiders brought to the young fluctuates during the nestling period, although it is difficult to observe any variation in the numbers at risk in the field. It is clearly a case of selection by the bird, rather than the number of foods available regulating the diet of the bird.

Opiliones. In the winter months these are found in some of the great tits, and in one bird in April. They were generally immature forms of two species, *Platybunus triangularis* (Herbst.) and *Nemastoma lugubre* (Mull.), and only in February 1950 were they found in any number, when four birds contained 15 *Platybunus triangularis*. In all, nine birds (6%) had eaten Opiliones, and they were not found in any of the other titmice.

Diplopoda. Fragments of millipedes (?*Polydesmus* sp.) occurred in three great tits and two blue tits in December, January, and April.

Pseudoscorpiones. Two great tits, one in January and one in September, contained a specimen of *Chthonius ischnochelus* (Herm.).

Isopoda. These were found in two instances in great tits. In February 1950 fragments of two *Philoscia muscorum* Scop. were found in one bird, and in April one *Porcellio* sp.

Acari. Mites of the family Oribatidae were found in all four species of tit, but most frequently in the blue tit. Two free-living species were identified, *Notaspis horridus* (Herm.) and *Carabodes labyrinthicus* (Mich.). Single individuals occurred in four great tits, and one coal tit, while one marsh tit contained seven. Eleven blue tits (4%) had taken mites, but only one bird had any number of these small animals; this was a bird from the December 1948 sample which contained 106 *Notaspis horridus*. Generally the mites were eaten during the winter months.

Excluding spiders, none of the other groups occurred in sufficient numbers to warrant attention as important foods, but their casual occurrence in the winter months may indicate that the birds were willing to eat a wider variety of foods at a time when other food is possibly more difficult to come by.

(*d*) *Grit and snail shell*

As there is some doubt as to whether snail shell is taken in lieu of grit, it was decided to treat these under the same heading. From Table 16 it can be seen that only the marsh tit takes grit regularly, and that the blue tit least frequently has stones in the gizzard. Observations at the nest have shown that both great and blue tits bring grit regularly to the young and this is clearly shown in the figures for the May samples (no coal or marsh tits were examined in this month, but there is no reason to suppose that they do otherwise).

It is difficult to correlate the consumption of grit with any particular diet, such as seed or vegetable tissue, for during the nestling period the birds are almost entirely insectivorous, and yet this is the time when most of them contain stones. The adult bird brings beak-fulls of grit to the nest and feeds a little to each of the young; it is not brought in accidentally attached to other food. The same applies to the feeding of snail shell to the young, and one pair of blue tits were seen to bring large pieces of dry snail

hell (perhaps from a thrush's anvil), showing that it is the shell and not the snail which s the important part of the food. It is likely that the mineral salts, in particular alcium, are necessary for bone growth, and also for egg laying, as the only time snail hell was found in marsh tits was in two females in April, and it occurred in two of the hree female great tits obtained in this month in 1949. An interesting feature at one reat tit nest in 1950 was the occurrence of hen egg shell in four of the five young xamined: as this nest was near the forest nursery the adult must have found the site f a picnic lunch.

Table 16. *Percentage occurrence of grit and snail shell*

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Great tit												
% with grit	36	26	50	15	0	0	92	11	0	0	9	17
% with snail	27	53	8	0	0	15	60	0	18	0	0	25
Blue tit												
% with grit	4	0	12	7	0	14	85	0	5	0	0	5
% with snail	0	0	0	0	0	5	71	0	0	0	0	0
Coal tit												
% with grit	20	33	92	0	50	50	—	0	0	25	67	63
% with snail	Nil						—					
Marsh tit												
% with grit	100 % except June and July						—	0	67			
% with snail	Nil except April				—	50	—					

Snails are found most frequently in the great tit, and where these could be identified ne species of importance was *Goniodiscus rotundatus* (Mull.), a common litter snail. These were sometimes found whole and apparently taken alive, which, together with he fact that apart from the breeding season the main snail eating months are October o January, indicates that the snail may form a source of food for this species. The bsence of snails in all the other species, apart from the breeding season, is very triking as small and immature specimens are common, so that size alone is not the ontrolling factor.

When snails were found in the birds they did not occur in any number, rarely more han two or three, and the volume of grit was also small.

(*e*) *Vegetable tissue*

Although oak bud tissue is found in the diet of the blue tit in 10 months of the year, part from the spring months it is present in only 9 % of the birds examined and then as ess than 5 % of the total contents. In fact it is mainly bud scales which may be taken ccidentally, and can have no food value. This applies also to the coal tit throughout he year, and to the great and marsh tits which, with the exception of the April ample, showed only traces of bud tissue in some of the spring and summer birds. n the spring samples (Feb., Mar., Apr.) of the blue tits the picture is very different. Of 54 birds examined only one did not contain bud tissue, and of these birds 34 contained volumes estimated at over 50 % of the total gizzard contents. In March and April 1949 the whole sample of 26 birds yielded no individual with less than 40 % otal volume as bud tissue, and 19 birds contained 75 % or over. Similarly, one great

tit in the seven examined in April 1949, and both marsh tits in this month, contained a considerable amount of bud tissue. It is necessary to point out that at this time of the year the april bud gall (*Neuroterus aprilinus*) was very abundant in the Forest of Dean, and it is difficult to separate bud tissue taken while searching for the eggs, larvae, and pupae from that which may have been taken for the plant tissue itself. An indication that the plant tissue may form an important part of the diet of the blue tit in February and March is given by the fact that cynipid larvae were found in only seven of the

Table 17. *The percentage occurrence of oak bud and oak gall tissue*

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
						OAK BUD TISSUE						
Great tit	0	0	0	0	50	39	28	11	0	0	0	0
Blue tit	8	20	31	93	100	100	15	29	5	0	0	5
Coal tit	0	17	8	100	0	100	—	100	50	13	0	0
Marsh tit	0	0	0	25	—	100	—	50	0	0	0	0
						OAK GALL TISSUE						
Great tit	64	73	67	69	0	8	0	0	45	100	36	58
Blue tit	64	60	65	27	88	100	6	0	91	92	94	68
Coal tit	80	83	92	25	0	0	—	0	100	100	83	100
Marsh tit	25	50	100	50	—	75	—	0	50	67	67	25

31 birds containing quantities of bud tissue. It is clear that the blue tit, in particular, finds a large part of its food in the oak buds during the spring months. No trace of bud tissue of any other species of tree was found in all the birds examined, although these were locally fairly plentiful (see Table 1).

Apart from small seed-like galls such as *Andricus ostreus* and *A. collaris*, which are generally taken whole, it was impossible to identify much of the gall tissue with any accuracy. The more fleshy galls are pecked at, and quickly break up into a mush of cells in the gizzard. During the months of May and June practically no galls are taken. In July and August the leaf galls of *Cynips* spp. are eaten by all four species, and these galls are found from then until the end of the winter months. In September and October the galls of *Andricus collaris* form the major gall food, followed in

Table 18. *Percentage of birds with more than 50 % gall tissue*

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Great tit	0	0	0	0	0	7	17
Blue tit	14	85	63	9	12	4	0
Coal tit	0	0	17	0	20	0	38
Marsh tit	0	33	0	25	0	0	25

November by *A. ostreus* and *Neuroterus lenticularis*, which continue to be taken in December and January. All the over-wintering galls are liable to occur during any of the winter months. From February until April the bud galls are taken but of these *Neuroterus aprilinus* in its later stages was the only one which could be identified. From Table 17 it can be seen that generally over half the total samples of all four species of titmice from July to January contain gall tissue. However, only 28 % of the great tits contain more than a trace of gall tissue during this period, as against 47 % of the blue tits, showing that it is of less importance in the diet of the former species. The blue tit

shows the greatest preference for gall tissue and the succession of *Cynips* spp. galls in July and August, with *Andricus collaris* in September and *A. ostreus* in November, is clearly demonstrated in this species. In January, when the other tits take quantities of galls, the species *Neuroterus lenticularis* is the most important one, and being found in the litter at this time of the year, is available to ground feeding birds only. The spring samples have not been included in Table 18 owing to the difficulty in identifying early stages of bud gall tissue, and hence in estimation percentage volumes. The April samples of all four species containing bud tissue yielded considerable numbers of the adult *N. aprilinus*, which were frequently found with unexpanded wings in the case of the blue tit samples, indicating that they were taken from the gall before emergence.

Table 19. *Percentage occurrence of nut tissue*

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Great tit	27	100	100	73	92	54
Blue tit	6	59	44	40	31	7
Coal tit	17	29	20	0	46	0
Marsh tit	60	75	100	0	25	0

The dominant tree being oak it was assumed that any nut tissue occurring in the birds from this region would probably be acorn. This was not so, however, as during the three winter periods studied different nuts were taken. In 1948–49 acorn was eaten, in 1949–50 sweet chestnut, and in 1950–51 beechmast, corresponding with the

Table 20. *Percentage of birds with different nut tissues*

	Sample size	Percentage birds with estimated volumes of		
		>5%	>50%	>100%
Great tit				
1948–49, acorn	13	31	38	0
1949–50, chestnut	32	13	25	19
1950–51, beechmast	29	3	24	66
Blue tit				
1948–49, acorn	28	4	7	0
1949–50, chestnut	51	4	6	0
1950–51, beechmast	50	0	18	52
Coal tit				
1948–49, acorn	8	50	13	0
1949–50, chestnut	19	5	5	0
1950–51, beechmast	14	0	0	29
Marsh tit				
1948–49, acorn	9	0	0	11
1949–50, chestnut	7	0	0	29
1950–51, beechmast	7	0	14	71

heavy cropping of these trees in these years. Although the beechmast crop was almost non-existent in the winters of 1948–49 and 1949–50, sweet chestnut was moderate in September 1950, and was still to be found in October, while acorns were fairly numerous in 1949 and 1950. It appears, therefore, that the order of preference in

selection of nuts is beechmast, sweet chestnut, and acorn. The great tit and marsh tit are the species most frequently found with quantities of nut tissue, and the coal tit the least. The drop in occurrence in December is not due to any change in the availability of nuts, but to the counter-attraction of an increase in insect food when the winter moth (*Operophtera brumata*) and associated species emerge. The preference of all species of titmice for beechmast is shown in Table 20. This is even more marked when the distribution of the three species of tree is taken into account. In the sample area of 12 acres in the Barnhill Plantation, where most of the birds were shot, oaks are 31 to the acre, sweet chestnut five per acre, and beech nil. The beeches are found almost entirely in the valley Bix Slade, and during the autumn and winter of 1950 the tits congregated in this area, presumably attracted by the mast crop. Birds shot in the oak woodland over half a mile away, feeding in oaks, were found to have gizzards distended with beechmast.

The grey squirrel (*Sciurus carolinensis*) is an important competitor for nuts, and is very common in this area. It can be of use to the birds by leaving half-eaten exposed kernels on the ground when disturbed, and in disturbing the snow cover, thereby

Table 21. *Percentage occurrence of* Viola, Oxalis *and* Betula *seeds*

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Viola												
Great tit	9	0	0	8	50	0	0	5	64	83	18	0
Coal tit	0	0	0	25	0	0	—	0	0	13	0	0
Marsh tit	25	0	0	25	—	0	—	0	33	33	20	25
Oxalis												
Great tit	36	67	58	69	50	15	0	11	91	100	64	33
Blue tit	0	0	4	0	0	0	0	0	0	0	0	0
Coal tit	0	17	15	0	0	0	—	0	0	0	17	0
Marsh tit	0	0	50	55	—	0	—	50	50	67	40	0
Betula												
Great tit	0	0	8	8	0	0	0	0	0	0	0	0
Blue tit	24	24	19	0	0	0	0	0	0	0	13	27
Coal tit	0	17	0	0	0	0	—	0	0	0	0	14

exposing the litter layer. This latter effect was seen in December 1950 when the squirrels 'opened up' much of the snow-covered ground under the beeches and enabled the birds to search for mast. Under these conditions of snow and frost when the moths *Operophtera brumata* cease to be available, the exposure of the litter layer is of great importance to ground feeding birds, and especially to the great tit.

May is the only month when seeds are not found in any of the tits, and of the four species the great tit, and to a lesser extent the marsh tit, are the main seed eaters. In these birds wood sorrel (*Oxalis acetosella*) and violet (*Viola canina*) seeds are most frequently found, while these occur only rarely in blue and coal tits. Birch seeds (*Betula pendula*) occur most frequently in blue tits. Of other seeds, one willow-herb seed and one grass seed were found in a blue and marsh tit respectively, alder seeds in two blue tits, and *Juncus* sp. in a blue tit which had been feeding on *Coleophora* larvae on this plant. Nettle seeds (*Urtica dioica* L.) were found in three blue and one marsh tit, in the former in large numbers averaging 260 per bird. Considering how common nettles are in Bix Slade, it is rather surprising that the seeds were found in

one month's sample only, i.e. November 1948. Generally the numbers of seeds per bird were small except in the following cases. In September six blue tits contained an average of 114 birch seeds, and in November and December six had an average of 30 seeds: the volume of this seed is, of course, small. In July ten great tits had an average of 18 *Oxalis* seeds and in August an average of 20, while the marsh tit peak in numbers of seeds was in January, with an average of 14. *Oxalis* is one of the dominant herb layer plants, while *Viola* is less common although the seeds are more conspicuous. In August five great tits averaged 13 *Viola* seeds and in July only six. The difference in quantity and in occurrence of *Oxalis* and *Viola* seeds in the great tit's diet appears to be dependent on the distribution of the plants rather than selection on the part of the bird. Only on two occasions were birch seeds found in great tits and then single seeds, although these winged seeds were very common in the litter layer near the trees. The small size of this seed seems to exclude it from the diet of great and marsh tits when feeding on the ground.

One of the more unusual foods revealed by the analysis of gizzard contents was the fruiting bodies of moss. Even stranger, that although there are several common mosses fruiting at various times of the year in the forest, only one of these species was taken, this being *Dicranoweisia cirrata*. This is found on fence posts, and tree trunks and boughs, and fruits in the winter months. Apart from one coal tit in November 1948, which contained a few sporogonia, and one marsh tit in January 1949 which contained 233, the blue tit is the main feeder on this material. The January samples of the first

Table 22. *The occurrence of moss sporogonia in blue tits*

		Oct.	Nov.	Dec.	Jan.	Feb.
Percentage birds with sporogonia	1948–49	—	56	100	88	0
	1949–50	0	25	0	90	10
	1950–51	9	25	18	25	—
Average no. of sporogonia per bird	1948–49	—	56	+	408	0
	1949–50	0	61	0	322	5
	1950–51	5	31	10	10	—

Note. + = <1.

two years contained so much sporogonial material that the gizzards and intestines were stained a vivid green, as was the alcohol into which they were placed. Each capsule measures about 2 mm in length and 0·5 mm in diameter, and the occurrence in such large numbers shows that they are deliberately 'cropped' and not taken by accident. During January 1950 eight sample pieces of moss were collected from different trees in the area, measuring from 2 to 12 cm^2, and the average yield of capsules was about 7 per cm^2. This also supports the view that a bird with 300 or 450 of these capsules could not have taken them accidentally. The spores are rich in oil, and if taken in sufficient numbers may be a valuable food source at this time of the year, or possibly they yield some necessary food substance. It is difficult to understand why the other titmice do not exploit this food source, unless it is excluded by the small size of the particles. A blue tit found dead in a garden at Hordley, Oxfordshire, in February 1949 was found to have 375 moss sporogonia of this same species, so that the habit may be general. Haftorn (1954), studying the crested tit (*Parus cristatus* L.) in Norway, records that this species was seen pulling at moss tips on snow-free rocks in December, probably eating the capsules.

Miscellaneous vegetable matter such as fragments of leaf or bark, or, in the case of young birds, of nest material is sometimes eaten. Occasionally in blue tits pieces of bark and dead wood with a fungal growth are found, and it is of interest to note that Newstead (1908) found four blue tits containing 'a black fungus'.

(*f*) *Discussion*

In this part it has been shown that in oak woodland the foods taken by the great and blue tits throughout the year are in general quite different and distinct so that there is no competition for food between these species. When the insect groups are similar, either the species taken are different, or else they are temporarily very abundant, as in the flush of caterpillars in the breeding season. The position of the coal and marsh tits is not so clear as their real habitat is not present, for the coal tit is primarily a bird of coniferous woods while the marsh tit is found mainly in woods with a shrub layer. The coal tit tends to take small free-living insects, and will concentrate on foods from trees other than oak, although these trees may not be common. The marsh tit shares certain features with both the great and blue tits, but in many ways its diet is nearer to that of the great tit, and in this habitat with no shrub layer, competition between it and the great tit may explain the few birds found.

THE ORIGIN AND NATURE OF THE INSECT FOOD

(*a*) *Sources of food*

A classification of insects taken by titmice, based on the habitats occupied by the insects, indicates the feeding stations of the four species of birds during the year. An analysis of the ecological separation of the birds, based on this type of data alone, is incomplete, as other factors, such as the species of food eaten, must be taken into account. However, this method does show that the titmice have certain preferred feeding stations, and it enables the data obtained from gizzard analyses to be compared with data obtained by other workers using field observations.

The insects found in gizzard analyses have been placed in habitat groups, using data from the literature and from observation. A winged insect may occur in any of the categories. If it is 'widespread', but most commonly found in one or two of the habitats, such cases have been included in the following analysis. It is necessary to emphasize that the divisions are not absolute, although this difficulty has been to some extent overcome by grouping. Even so, there are obvious drawbacks. For example, defoliating caterpillars are usually found on the twigs and leaves, but they may fall to the ground if disturbed, or for pupation. In this analysis only those insects which could be identified down to species have been used, except in a few cases where only the genus was determined, but all the members of the genus frequent the same habitat. Hence the total numbers of insects are smaller than the total numbers present in the birds.

It is clear from Table 23 that the great tit obtains a much higher proportion of its insect food from the ground and herbage than do any of the other titmice, and that the blue tit rarely takes insects from the ground. The percentage of 'widespread' insects is high for both the great and marsh tits, and consists almost entirely of adult insects

which emerge from pupae in the ground or litter. In both these cases, it is likely that the insects are in fact taken on the ground, and hence the figures in category *a* should probably be much higher than shown in the table. The blue tit, and to a lesser extent the marsh tit, obtain most of their food from the twigs, buds and leaves, while the coal tit feeds more on the trunks and branches.

Table 23. *Percentage of insect food of titmice taken from the habitats*

		Great tit	Blue tit	Coal tit	Marsh tit
a	Ground and litter	9·1	0·1	2·1	3·1
b	Low herbage	5·1	0·6	+	0
c	Trunks and branches	7·4	9·6	40·0	0·1
d	Twigs	0·5	30·8	17·0	27·1
e	Buds	0·6	27·6	1·5	17·9
f	Leaves	15·6	17·2	21·9	18·6
ac		1·5	0·4	0·1	1·8
cd		3·0	2·8	5·2	0·5
df		9·5	2·8	3·0	13·1
g	Widespread	47·7	8·1	9·2	17·8
Total of insects		3264	12 524	3347	866

Note. + = <0·1%.

It is convenient to group some of the habitats for a seasonal comparison of the feeding stations of the birds, and in Fig. 2, ground and low herbage have been combined, as have trunks and branches, while twigs, buds and leaves have been placed in a joint category. In winter the great tit is taking most of its food from the ground, and from tree trunks and branches. It is likely that the moths *Operophtera brumata* and *Erannis* spp., which emerge from pupae in the ground and climb the trees to lay their eggs at this time, are taken on the ground by the great tit, although they have been included in the 'widespread' category in the figure, and are responsible for the large value of this group for all the tits in December. In the blue tit these moths are probably taken from the twigs, as they occur with other foods from this source. The blue tit is mainly feeding on the twigs in the winter, but is also taking oak-leaf-mining larvae and pupae from dead leaves. Both the blue and coal tits show increased feeding activity on tree trunks in January, while the marsh tit takes little food from this source, and eats more ground forms than these two species.

During the spring the great tit again shows a high figure in the 'widespread' category, due to the presence of adult sciarids and bibionids in its diet in February and April respectively. These insects all emerge from the ground and litter layer, and are likely to be taken here, as they are associated with other ground forms. This applies to the marsh tit in February also. The general pattern is much as in the winter, with the blue tit feeding mainly on the twigs and buds. In February and April, bud feeding by this species shows a marked increase, nearly 90% of its insect food being bud-inhabiting forms. The coal tit is still concentrating on trunks and branches, and the marsh tit on probable litter forms, and twig and bud species. All four titmice take a greater proportion of their food from the oak buds in April, and even the great tit is beginning to feed more in the canopy, a trend which increases in the next two months.

All species of titmice in the summer months are feeding on insects found on the leaves, but even in the breeding season in May, the great tit is taking a smaller

proportion of leaf forms, and it must be remembered that in this month it takes a considerable number of ground spiders, so that many of the insects in the 'widespread' category may be taken on the ground. The 'widespread' group in summer months is largely composed of beetles, which may be present in any of the habitats, but when they occur in association with insects taken from herbage, as in the great tit in July, or with twig and leaf forms, as in the other species, there are reasonable grounds to assume that they are taken from these sources also. The absence of ground insects in the marsh tit is striking, as this species is taking seeds in July, but some of the insects in the 'widespread' group may well be taken on the ground, as in the great tit. During the summer, the great tit is the only species of tit taking ground and herbage insects, and in July the largest proportion of its food is probably taken from this source.

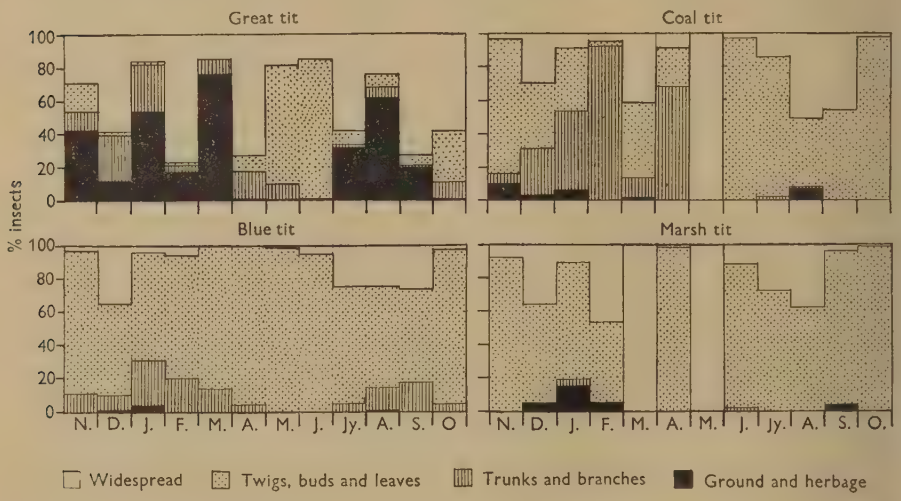

Fig. 2. Percentage of insects taken by titmice from the different habitats.

In the autumn, ground feeding by the great tit is still pronounced in August and September, and again the 'widespread' category insects are probably taken here also, for in the later part of the season the great tit is taking nuts as well as seeds from the ground. The October figures for the *def* group are high for all species except the great tit, as the blue tit is taking leaf-mining larvae, while the coal and marsh tit food is dominated by the sycamore aphis. The great and marsh tits in October are also taking leaf-weevils, which may be in the litter at this time, although they have been included in the *def* category in the figure. During the autumn, therefore, the high proportion of food taken from the twigs and leaves is not necessarily correlated with any similarity in the diets of the titmice.

From this analysis it will be seen that the feeding stations occupied by the great and blue tits are distinct during most of the year, as the great tit is largely a ground feeder, except in the breeding season, while the blue tit feeds mainly on the twigs, buds and leaves. The results shown in Fig. 2 are based on insect foods only, and the separa-

tion is even more pronounced when other foods, such as seeds, nuts and spiders, are included. The coal tit from November to April spends much of its time feeding on tree trunks and branches, while the marsh tit takes food from the ground and twigs. These results agree in general with the findings of Hartley (1953) and Gibb (1954*a*), who have studied the feeding stations of the birds in mixed woodland by field observations. In this latter type of habitat, however, the variety of food sources is much larger, and therefore it is difficult to make a direct comparison. It is known, for instance, that the birds will exploit temporarily super-abundant foods such as aphids or nuts, which vary from year to year on different species of trees. Colquhoun & Morley (1943), studying the different zones occupied by birds in oak woodland near Oxford by field observations, state that, in winter, the blue tit was most frequently seen in the 'tree zone' (i.e. the canopy between 15 and 35 ft), while the great tit mostly frequented the 'shrub zone' (i.e. 4–15 ft). As the great tit generally moves into the shrub layer when disturbed, and also frequents this place when hammering food taken from the ground, it is suggested that these observations may not show the true feeding station of this species.

(*b*) *Size of insects eaten*

Body length has been taken as the criterion of the size of each insect species, and the mean value of variations in the length of a species given in the literature has been used. The sizes have been divided into 2 mm groups, and it is obvious that only those insects which could be identified to specific rank can be used in an analysis of this kind. Numbers are therefore much smaller than the total of insects found in the birds. Larvae have not been included, as the length varies with the stage of development, and the gizzard material is often too fragmentary to be measured. The exclusion of larval forms reduces the true percentage proportion of small foods in the blue tit, as in the autumn and winter this species takes very large numbers of small larvae (mostly of species measuring up to 4 mm). The results of a comparison of diets based on the size of insects eaten show that the four species of titmice have different preferred size-ranges of insect food.

Table 24. *Percentage composition of the diet of titmice based on the size of insects taken*

	Insects of body length				Total of insects
	0–2 mm	3–4 mm	5–6 mm	>6 mm	
Great tit	26·5	19·6	21·9	32·0	2553
Blue tit	58·7	29·2	2·6	9·5	6507
Coal tit	73·6	16·6	3·1	6·7	2389
Marsh tit	22·2	51·7	15·5	10·6	730

In general the blue tit takes small insects, and those over 6 mm are almost entirely the moths *Operophtera brumata* and *Erannis* spp., taken in winter. The 2 mm group in the great tit is composed of lepidopterous eggs (mostly *Orgyia antiqua*) in the winter, and aphids taken in June, so that throughout the year the major part of its food is over 5 mm long. The coal tit takes a larger proportion of very small insects than any

of the other titmice, nearly three-quarters of its food being under 2 mm, and most of the insects over 6 mm are moths, as in the blue tit. The marsh tit takes insects which are intermediate in size between those taken by the great and blue tits, and 67 % of its food is in the 3–6 mm group. The upper size limit is well defined, as only three adult insects of over 15 mm were found in the blue tit, although it is known from observations at the nest that caterpillars exceeding this length are brought to the young. In the great tit 28 insects (1·1 %) were over 15 mm, of which three moths and one tipulid were over 23 mm. Again it is known that particles of this size are brought to the young in some numbers during the last few days of the nestling period, and that foods measuring up to 30 mm are brought occasionally (see Table 26). In the coal tit 11 insects of over 15 mm occurred, of which six were female long-horned grasshoppers *Meconema thalassina* (Deg.), in the 20–22 mm group, which were found in two birds. This indicates that although the coal tit generally prefers small insects, it is capable of taking large soft-bodied ones. Only one adult insect over 15 mm was found in the marsh tit.

As all the titmice can hammer food, it is surprising that the upper size limit is so pronounced, especially in the blue tit. The smallest insect foods eaten by the great tit are aphids, and the eggs of the vapourer moth, and it is significant that both these items are found in clusters, and presumably are worth taking on this account only. The differences in the size of insects taken by the great, blue and coal tits are in accordance with the relative sizes of the birds; but the marsh tit, which is about the same size as the blue tit, generally eats larger insects than this species.

In general the beak of a bird is adapted to its mode of feeding (Lack 1947), and these adaptations are seen within the genus *Parus*. The average beak-lengths of 20 birds of each species were measured, the length being taken from the tip of the upper mandible to the hinge where it joins the skull. The measurements for the great, blue, coal and marsh tits were 13·3, 9·1, 10·8 and 10·8 mm, respectively. These measurements were made on freshly killed specimens, and are slightly larger than the figures given by Witherby, Jourdain, Ticehurst & Tucker (1938). The beak of the great tit is not only the longest, but also the stoutest of the long-billed species of titmice, and its major foods are large insects, seeds and nuts. The blue tit, on the other hand, has a short but very stout beak, suited to tearing and hammering. Its short length suggests that small foods are taken, which is borne out by the analysis in Table 24, and the habit of the bird of taking foods which have to be extracted from galls, buds, leaves or dead wood, is shown by the following figures. In a total of 13 576 insects found in blue tits, 5066 (37·4 %) were cynipid and cecidomyid larvae from within oak galls and buds, and leaf- and wood-mining larvae. In addition, scale insects have to be torn off twigs, and if these insects are included, the figure becomes 8646 (63·8 %), clearly demonstrating the feeding habits of the bird, and the correlation of the beak structure with these habits. The average beak-length is the same in the coal and marsh tit, but the beak of the coal tit is thinner, and more typical of an insectivorous bird, and we know that this species feeds largely on very small insects. The beak of the marsh tit is stouter and more like that of the great tit, and its diet shows many features in common with that species, but as would be expected from the shorter length of the beak, the insects taken are smaller than those eaten by the great tit.

The occurrence of two, or more, species of birds frequenting the same feeding stations may not be indicative of competition for food, even if there is no apparent superabundance, for the actual food taken by the birds may be differentiated by size or habit. For example, one of the bird species may be adapted to take a small insect from the surface of a leaf, e.g. the coal tit, another to tear the leaf and extract a larva, e.g. the blue tit, and yet another to take a large insect from the leaf surface, e.g. the great tit. A more detailed analysis down to the species of food eaten is therefore essential.

THE FOOD OF NESTLINGS

In 1951 the foods brought to the young of one brood of great tits and one brood of blue tits in Nagshead Plantation were studied by means of glass-backed nest-boxes placed against a hide in which the observer was later concealed. The interior of each box was illuminated by a window in its roof, and at an observational range of about 9 in. it was possible to identify most of the foods brought by the adult birds.

(*a*) *Great tit*

Seven of the young hatched on 30 May, and the remaining two on 31 May; all nine fledged on the morning of 18 June. The hatching dates were about average as compared with other nests in adjacent nest-boxes. The young were observed on the average for more than six hours a day during the 20 days of the nestling period. The daily periods of observation were varied to give a comprehensive picture of the feeding activity during the nestling period, sometimes being started from the first dawn feed, sometimes in the middle of the day, and sometimes during the late afternoon continuing up to the time of the final feed. An account of the feeding rates, and the behaviour of the adult and young great tits has been published elsewhere (Betts 1955). The composition of the diet is shown in Table 25.

Table 25. *The diet of a brood of great tits in 1951*

	No. of food items observed	Percentage of total diet	Changes in percentage composition of diet from 30 May to 18 June: Nestling days 1–2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20
pidoptera larvae	3869	63·7	76	44	33	61	78	72	79	68	51	47
pidoptera pupae	411	6·8	1	1	2	4	3	10	5	10	17	22
pidoptera imagines	179	2·9	0	0	0	0	0	0	0	3	21	22
miptera	285	4·7	2	15	19	9	3	1	0	0	0	0
leoptera	611	10·1	1	12	21	17	10	8	6	10	3	4
ptera	83	1·4	2	3	4	3	1	+	+	1	1	+
iders and egg cocoons	528	8·5	16	23	17	4	3	8	9	7	4	2
ails and grit	80	1·4	1	2	2	1	1	1	1	1	2	2
her insects and indet.	35	0·5	1	+	2	1	1	+	+	+	1	1

Note. + = <1%.

Lepidopterous larvae were the main food but adult insects formed over 19% of the diet, and spiders were also brought regularly. The caterpillars were mainly the larvae of the winter moth (*Operophtera brumata*) and tortricoids, 46% of all the caterpillars brought to the nest being *O. brumata*, and 36% tortricoids. Other larvae, mostly Caradrinidae and some *Erannis* spp., were also brought to the young. The pupae were

tortricoids, and the moths mostly the wingless female vapourer moth (*Orgyia antiqua*), brought towards the end of the nestling period. The Hemiptera were almost entirely the brown scale (*Eulecanium coryli*), while the Coleoptera were represented by the silphid *Xylodrepa quadripunctata*, and the elaterid *Athous haemorrhoidalis*. The Diptera were tipulids and bibionids. Crushed snails and grit were brought to the nest on the average twice daily, each beak-full being shared amongst approximately half the brood, so that each nestling probably received a portion of these foods each day. The composition of the diet agrees fairly closely with that found in nestling great tits collected from this area in 1949 and 1950 (see p. 291), and also with similar observations in a mixed wood at Wytham in 1949 and 1950, collected by Hartley & Betts (unpublished), except that in the latter case slightly fewer adult insects were fed to the young.

From Table 25 it will be seen that the proportions of different foods brought to the young great tits varied during the 20 days of the nestling period, in particular scale insects, beetles and spiders formed a larger part of the diet in the first week than later. There appeared to be little variation in the proportions of different foods brought at different times of the day. Lepidopterous larvae formed less than half the total foods brought in the third to seventh days of the nestling period, corresponding with the peak in the proportion of other foods. From the eighth day the proportion of caterpillars in the diet increased, varying from 60 to 84 %, until the last three days of the period when it dropped to 50 % or less. The proportion of pupae in the diet remained small for most of the period, but increased to a maximum of 25 % of all foods on the nineteenth day. Female vapourer moths were brought only during the last six days, and on the last morning formed 48 % of the food.

Some of the changes in the diet can be correlated with changes in the foods available to the birds. The female vapourer moths, for example, were not observed on the tree trunks until mid-June, and even then they did not appear to be common. An examination of over 100 tree trunks up to a height of 8 ft yielded only six cocoons, but possibly they were commoner at a greater height, for on the nineteenth evening the adult great tits brought these moths to the nest at an average rate of one every 2½ min. The number of available tortricoid pupae increased steadily during the period, while the larvae of the winter moth decreased as they were beginning to pupate from about mid-June. These larvae pupate in the ground; the tortricoids, however, remain as pupae on the leaves, and hence are still available to the birds. The population of *Operophtera brumata* larvae was at a maximum during the early part of the nestling period, but larvae of this species were still beaten from the trees, in some numbers, as late as 24 June.

At the time of the maximum abundance of *O. brumata* larvae, the number brought to the young great tits attained a maximum of 69 % of the total foods on the second day of the nestling period. It then dropped to less than 30 % until the twelfth day when it rose to 43 %, falling away again until, on the last morning, no *O. brumata* larvae were brought to the nest. Nine samples totalling over 1000 oak leaves, collected from nearby trees on 3 and 8 June (nestling days 5 and 10), yielded about four *O. brumata* larvae per 100 leaves, and this species formed 59 % of all defoliating larvae present in the samples. At this time *O. brumata* larvae formed less than 30 % of all

foods brought to the young, and only 37 % of all caterpillars brought. It appears, therefore, that the great tits were not selecting this food in proportion to its abundance in the habitat.

The scale *Eulecanium coryli* was present on the twigs in large numbers throughout the nestling period, but it was not brought to the young after the eleventh day. The small size of this food (about 4 mm) may make it a less attractive food as the young increase in size, for after reaching a maximum of 22 % of all foods on the fifth day, the proportion of this food fell steadily until the eleventh day, when it formed only 2 % of the foods brought. The varying number of spiders brought to the young did not appear to be correlated with any observed changes in the spider population, but no direct measurement was made.

In conclusion, it may be stated that an analysis of the food of nestling great tits in oak woodland demonstrates the very mixed diet of this species. The selection of this diet does not necessarily correspond with the abundance of any one species of insect, for the larvae of *Operophtera brumata* were not exploited as fully as might have been expected from the numbers present on the oak trees. Tinbergen (1949) found that in pine woods in Holland titmice brought relatively fewer larvae of *Panolis griseovariegata* (Goez.) and *Acantholyda pinivora* Ens. to their young in years when these larvae were common, than in years when they were scarce. Similarly, Steinfatt (1941) found that during a plague of the nun moth (*Lymantria monacha* (L.)) in East Prussia, these larvae rarely formed more than 50 % of the food of the titmice. Tinbergen's conclusion that titmice prefer a varied diet is therefore supported by the present data on the food of nestling great tits in oak woodland.

The variations in the proportions of different-sized food items are shown in Table 26, which shows clearly that the size of items brought to the nest increases as the young grow older. The predominance of foods measuring under 9 mm in the

Table 26. *The percentage of different-sized food items brought to the young*

Length (mm) ...	4	6	9	12	15	18	21	24	27	30	Total analysed
Day 1–5	17	20	27	28	7	+	0	1	0	+	1028
6–10	10	5	10	17	48	9	1	+	.	.	1882
11–15	1	6	9	9	62	7	4	2	+	.	2036
16–20	1	3	17	6	31	9	12	20	1	+	988

Note. + = <1%.

earlier part of the nestling period corresponded with the large numbers of scale insects and spiders in the diet at this time. During the first two days 65 % of the foods measured 9–12 mm, consisting mainly of the larvae of *O. brumata*. The population of this species was generally in the later instars of larval development at this time, with individuals measuring 15–18 mm., so that the birds were clearly selecting from the general population those individuals of smaller size. From the sixth day the major proportion of the food items measured about 15 mm, but items over this length were brought in steadily increasing numbers, until, on the last morning, 67 % of the food items measured over 20 mm. Observations at nests in Dutch pine woods by Tinbergen (1949) show that caterpillars of less than 10 mm in length are not taken by

titmice for their nestlings except during the first five days, although larvae under this size were present in the environment. These results agree with the present data in oak woodland. (After the fifth day the food items under 10 mm in length were spiders and insects other than caterpillars.)

(*b*) *Blue tit*

Six young hatched on 7 June, and the remaining two on 8 June, but one young bird died between 10 and 14 June, leaving a brood of seven. The hatching dates are slightly later than the average dates for blue tits in this area in 1951. The male unfortunately deserted the nest after the morning of 19 June when the birds were caught and colour-ringed to aid identification. The nest was under observation for an average time of 2½ h from the seventh to twentieth days, the young fledging before 0600 h G.M.T. on the twenty-first morning (27 June).

Table 27. *The diet of a brood of blue tits in 1951*

	No. of food items observed	Percentage of total diet	Changes in percentage composition of diet from 13 to 26 June: Nestling days 7–8	9–10	11–12	13–14	15–16	17–18	19–20
Lepidoptera larvae	345	19·0	64	36	29	33	17	12	8
Lepidoptera pupae	1295	72·0	19	48	59	62	74	79	86
Spiders and egg cocoons	113	6·3	16	12	12	3	4	6	4
Snails and grit	33	1·9	1	4	0	0	4	2	2
Other insects and indet.	14	0·8	0	0	0	2	1	1	0

The composition of the diet is shown in Table 27. The main food of this brood of blue tits during the period studied was tortricoid pupae. Of the lepidopterous larvae 30 % were tortricoids, 28 % *Operophtera brumata*, and 23 % Caradrinidae, with *Erannis* spp. and other 'geometrids' forming the major part of the remaining 19 % of the larvae. Moths and other insects formed less than 1 % of all the foods brought to the nest, but spiders, crushed snails and grit were brought regularly. As this brood hatched later than most of the blue tits in this area, and observations were not begun until mid-June, it is difficult to compare the diet with the foods found in nestling blue tits collected in the same area in May 1949 and 1950. As would be expected, the proportion of tortricoid pupae was much higher in this late brood (72 % compared with 20 % found in the 1949, 1950 nestlings), and consequently the proportion of lepidopterous larvae was much lower (19 % compared with 56 % in 1949, 1950). The proportion of spiders, and the very small number of adult insects (other than scale insects) are features common to the diet of nestling blue tits in all three years.

Comparing the diet of this brood with that of adult and juvenile blue tits in June 1949 and 1950, it is seen that whereas aphids formed the greatest proportion of the food of this species in these years, they were not brought to the nestling blue tits in June 1951, although present on the leaves at the time. The small size of aphids may make them less attractive as food for the nestlings when other larger items, such as pupae, are abundant. The proportion of lepidopterous larvae fell steadily during the period while the proportion of pupae rose, reaching a maximum of 88 % of all foods

on the twentieth day. The pupation of *Operophtera brumata* began in mid-June, and these larvae were not brought to the nest after 23 June. Spiders formed a more important part of the diet during the earlier than the later part of the period.

The distribution of the different food item sizes brought to the young during the seventh to twentieth days of the nestling period is shown in Table 28. During the period studied most of the food brought to the young was in the 9 mm group, and there was no gradual increase in the size of foods brought with increasing age of the young, as observed in the great tit foods.

Table 28. *The size of food items brought to the young*

	Length (mm)									
	5	7	9	11	14	16	18	23	27	32
No. of items	13	30	1388	19	56	33	121	73	35	7
Percentage of items	0·7	1·7	78·0	1·1	3·2	1·9	6·9	4·1	2·0	0·4

(*c*) *Comparison of the foods of a great and blue tit brood*

As the young blue tits hatched eight days later than the young great tits, the period of overlap of the two broods was short, but during the six days that both broods were observed the foods brought to the young by the adult great and blue tits showed certain marked differences, which are demonstrated by the figures given in Table 29.

Table 29. *A comparison of great and blue tit nestling foods from 13 to 18 June 1951*

	Great tit		Blue tit	
Nestling days	15–17	18–20	7–9	10–12
	Percentage of diet			
Lepidoptera larvae	66	42	58	27
Lepidoptera pupae	12	17	23	61
Lepidoptera imagines	6	32	0	0
Other insects	7	5	0	0
Spider and egg cocoons	7	2	17	11
All other food	2	2	2	1

The main difference lies in the proportions of pupae and adult insects brought to the two broods. The blue tit brought a much greater proportion of pupae than the great tit, while the great tit brought a larger proportion of moths and other adult insects. The proportion of spiders was higher and caterpillars lower in the diet of the blue tit than in the diet of the great tit at this time.

The difference in the foods is reflected in the size of the food items brought to the young during these days. Most of the items selected by the great tit measured over 10 mm, while most of those selected by the blue tit measured under this length. It might be argued that the difference in the ages of the young of the two species affected the choice of item size (the blue tits being younger), but when the blue tits reached the comparable age of 15–20 days most of their food still measured under 10 mm. The percentage of this size group varied from 83% of all blue tit nestling foods on the

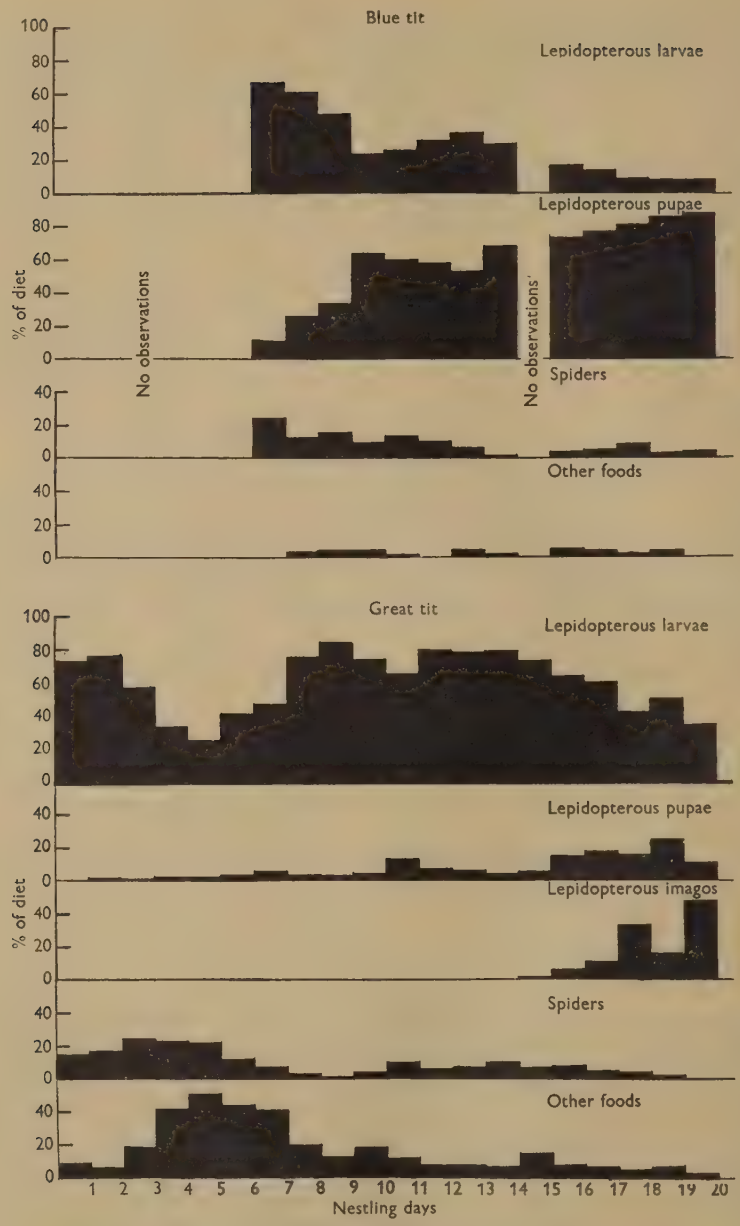

Fig. 3. The food of nestling great tits and blue tits.

sixteenth day, to 92% on the twentieth day. The composition of the nestling diets of the two species is shown in Fig. 3. In general, the selection by the great and blue tits of different foods for their young reflects the difference in the type of foods chosen by

the two species during the rest of the year, as described in the earlier part of this paper. The blue tit takes smaller food items than the great tit, and is better adapted than the great tit to extracting a tortricoid pupa from the centre of a curled leaf, a habit clearly shown by the large numbers of pupae brought to the young.

NUMERICAL RELATIONSHIPS BETWEEN TITMOUSE AND WINTER MOTH POPULATIONS

An attempt was made to calculate the effect of predation by the titmice in the Forest of Dean on the population of the winter moth (*Operophtera brumata*) in its larval and adult stages, and to compare the predation in the nest-boxed area of Nagshead Plantation with that in the control area of Barnhill Plantation. No laid eggs of *O. brumata* were found in any of the gizzards of the titmice, and the pupae were not available to the birds as pupation takes place in the soil. The populations of adult and young titmice in an area of 55 acres in Nagshead, and in a sample block of 28 acres in Barnhill, were estimated in the breeding seasons of 1950 and 1951. Estimates of the numbers of caterpillars eaten by the titmice were compared with those of the populations of defoliating caterpillars in the two areas. It will be shown that although *O. brumata* was one of the chief foods of titmice, the effect of predation by these birds on the caterpillar populations, and on *O. brumata* in particular, was negligible in the two years for which measurements were made. Estimates of the populations of adult winter moths in the two areas in the winter of 1950–51 were also made. As there was no accurate method of estimating the population of titmice at this time, only general conclusions, derived from a comparison of data from gizzard analyses of the birds with data on the moth populations, could be obtained.

(*a*) *Estimation of defoliating caterpillar populations*

The population of defoliating caterpillars was estimated by a modification of the method devised by Schwerdtfeger (1931). The method consisted of sampling the amount of caterpillar frass falling from the trees by collecting it in trays of a known area. From data on the average defecation rate of the larvae, the average canopy size of the trees and the density of the trees per acre, it was possible to estimate the population of defoliating caterpillars per acre of woodland. An alternative method of counting the number of defoliating caterpillars in leaf samples, and expressing the results as the number of larvae per 100 leaves, was also used to compare the relative densities of the caterpillars in the two years, and to give the proportions of different species of larvae in the total populations. In this experiment, oblong trays of American cloth, suspended horizontally from wire pegs at each corner, and measuring 0·2 m^2, were used to collect the frass. Two or three trays were placed at random beneath the canopies of sample oak trees and left in position for periods of 1–1½ h. The number of caterpillar faecal pellets in the trays was counted, and the average number of pellets falling over 1 m^2 of canopy-covered ground in 1 h was calculated. As the faecal pellets are so small compared with the leaf surfaces, it is reasonable to assume that on dry windless days pellets fall at random beneath the canopy. Frass was collected only on such days, and the trays were not erected until the dew had dried from the leaves,

as the moisture might make small faecal pellets adhere to the leaf surface, and later, as the leaves dry, cause an abnormally heavy fall of frass. In 1950 four frass collections were made during the period 17 May to 13 June, so that an estimate of the caterpillar populations at the period of maximum abundance could be obtained. In 1951 it was possible to judge this period by observation, and frass was collected in the two plantations on only one day.

It was thought that the defecation rate of the caterpillars might be very variable, depending on the species of larva, the stage of larval development, the time of day and the climatic conditions. Consequently, in 1950, leaf sprays on the sample trees were enclosed in muslin cages for the period of frass collection beneath these trees, and the average defecation rate of the caterpillars was calculated from the numbers of pellets, and larvae, in these controls. As the variation was not as great as expected, in 1951 fewer controls were used. In both years the average defecation rate of 130 defoliating caterpillars of several species, over periods of 1–4 h on different days, was 1·9 pellets per hour, although the defecation rate of individuals of different species varied from 0·9 to 3·2 pellets per hour. An average rate of 2 pellets per hour has been used throughout the following calculations.

The area of ground covered by the canopy of each oak tree was estimated by measuring the diameter of the canopy at its widest point, and the diameter at right angles to this line; the mean radius was then calculated from the sum of these two values. The densities of the oak trees in each plantation were obtained from a total count of trees in sample blocks of over 6 acres and 12 acres in Nagshead and Barnhill respectively, and were found to be 63 per acre in Nagshead, and 31 per acre in Barnhill. For the purpose of estimating the caterpillar populations per acre of woodland, the average area of canopy-covered ground per acre has been derived from the average canopy area of the 34 trees sampled in each plantation, and the density of the trees. The number of pellets falling over 1 m^2 of canopy-covered ground has been calculated from the mean value of the numbers obtained from a sample of 18 trees in both Nagshead and Barnhill on two days in 1950, and from 16 trees in each of the two areas on one day in 1951. The final figures for the estimated populations of all defoliating caterpillars work out in Nagshead at 1 229 000 larvae per acre in 1950 and 558 000 larvae in 1951, and in Barnhill at 932 000 and 339 000 larvae per acre in these years. In 1951, therefore, the population was well below that of 1950, falling to 45 % of its 1950 value in Nagshead and to 36 % in Barnhill.

These estimates of the caterpillar populations per acre of woodland give, and are intended to give, only the general order of size of the populations, for no account could be taken of small trees and shrubs. However, the number of defoliating caterpillars on these shrubs involves only a very small proportionate increase in the size of the total population. A test of the accuracy of these estimates can be made by comparing the numbers of defoliating caterpillars per 100 leaves in samples collected from the oak trees in the two years. In 1950, 15 samples totalling nearly 3000 leaves yielded an average of 10·4 caterpillars per 100 leaves; in 1951, 28 samples totalling over 8000 leaves yielded 3·9 caterpillars per 100 leaves. On this basis, therefore, the caterpillar population in 1951 was only 38 % of that in 1950, a figure very close to that of 40 % derived from the estimates of the total populations in the two years.

The proportion of *O. brumata* larvae was obtained from samples of the caterpillar populations. In 1950, 215 out of 299 caterpillars were *O. brumata* (72%), and in 1951, 232 out of 375 caterpillars (62%). The proportion of this species in the Barnhill population was possibly smaller than in Nagshead, but the number of samples from each area was too small for a valid comparison. Neglecting this point, the estimates of the numbers of *O. brumata* larvae per acre in the two plantations work out in Nagshead at 885 000 larvae in 1950, 346 000 larvae in 1951, and in Barnhill at 671 000 and 210 000 larvae in these years.

The total caterpillar population per acre in the nest-boxed area of Nagshead was considerably higher than that in Barnhill, due to the higher density of trees rather than to heavier caterpillar populations per tree. In neither 1950 nor 1951 was there any visible defoliation of the oaks (but the degree of defoliation is probably not a reliable means of estimating caterpillar populations as it depends on the stage of development of the leaves at the time when the caterpillars hatch, and on the subsequent growth-rates of both larvae and leaves).

(*b*) *Estimation of titmouse populations in the breeding season*

Estimates were made of the numbers of adult and young titmice per acre of woodland in the two plantations at the time of the maximum abundance of the caterpillars in 1950 and 1951. The figures for the population in Nagshead are taken from data supplied by Dr B. Campbell and students at the Forester Training School, Parkend, co-operating in a general inquiry on nest-box populations (Lack 1955). The populations of titmice in Barnhill in each year were estimated by the writer in complete counts of tit nests in a sample block of 28 acres. The nests were located by noting the position of singing males at dawn during the periods of egg-laying and incubation, and each nest was checked later when the adults were carrying food to the nestlings. The brood-sizes were assumed to be the same as the average in the adjoining nest-boxed area. The total populations of adult and young titmice combined, at the time of maximum caterpillar abundance, were in Nagshead 13 per acre in 1950, 15 in 1951, and in Barnhill six per acre in both years. The average density of titmice was, therefore, more than twice as high in the nest-boxed area of Nagshead as in the control area of Barnhill.

(*c*) *Effect of predation by titmice on the caterpillar population*

The nestling period of the titmice coincides approximately with the maximum abundance of defoliating caterpillars. The amount of food eaten by one titmouse during this period was calculated from the average quantity of food given to each young bird during the last 10 days of the nestling period discussed previously. It has been assumed that an adult eats the same amount as a young one, and gizzard analyses of adult and young suggest that this is roughly true, though Gibb (personal communication) states that from field observations adults probably eat rather more per day than nestlings.

The average number of food items eaten per hour was six by each young great tit, and eight by each young blue tit, and the average time between the first and last feeds

of the day was 16 h. Taking a mean value of seven food items per hour, the number eaten per titmouse in the nestling period works out at 2240. From gizzard analyses of the two species from this area in 1950, 64% of the food of the great tit and 53% of that of the blue tit consisted of lepidopterous larvae and pupae, so that taking an average value of 60%, the number of larvae eaten by each titmouse during the nestling period was 1344.

From the figures given for the populations of titmice and caterpillars per acre of woodland it was possible to calculate the proportion of the caterpillar population probably eaten by the titmice. In 1950 this was 1·4% in Nagshead and 0·9% in Barnhill. The proportion of *O. brumata* larvae in the diets of titmice in 1950 was 24% of all identified caterpillars and pupae, and the predation on this species by titmice was about 0·5% in Nagshead and 0·3% in Barnhill.

In 1951, 71% of the food of the great tit and 91% of that of the blue tit consisted of lepidopterous larvae and pupae, so that taking an average of 80%, the number of larvae eaten by each titmouse during the nestling period was 1792. The proportion of the caterpillar population probably eaten by titmice was therefore 4·8% in Nagshead and 3·2% in Barnhill. The proportion of *O. brumata* larvae in the diet of the titmice was 33%, and the predation by the titmice in this year was about 2·6% in Nagshead and 1·7% in Barnhill.

On a basis of caterpillars per 100 leaves, the population in 1950 was probably less than half the size of that in 1949, while in 1951 it was only about one-fifth of the 1949 population, hence, even in 1951, with a relatively low density of caterpillars, predation by titmice did not exceed 5%. Although the population of titmice was twice as high in the nest-boxed area of Nagshead as in Barnhill, the proportion of the caterpillar population eaten by titmice in the two areas differed little, because the density of trees and shrubs, and hence of larvae, is much higher in Nagshead than in Barnhill. In Nagshead, as a result of these natural features and the presence of nest-boxes, the breeding populations of other species of birds (pied flycatcher, redstart, nuthatch, warblers, etc.) were also higher than in the more open Barnhill area. Predation by these other species of birds on the caterpillar population was not measured.

(*d*) *Estimation of adult winter moth populations*

The 18 trees which had been used for sampling the caterpillar populations in each plantation in 1950 were banded with a standard fruit-tree grease in the autumn of that year. This grease was brushed on to the tree trunks at a height of some 3 ft above ground-level, and formed a thick sticky band about 9 in. wide. The wingless female winter moths climb the trees to lay their eggs on the twigs and are trapped in the grease band. The traps were examined daily during the peak time of emergence of the moths, and at approximately weekly intervals during the beginning and end of the period. At each inspection the number and species of moths were counted, the insects removed, and the grease renewed if necessary. The number of winged male moths trapped in the grease at the peak period of emergence was sometimes so large that the surface of the band was covered, and it was essential, therefore, to remove these insects daily. Casual observations of the trees at night gave no indication that the female

moths avoided the grease bands, but as a check on this possibility, five ground traps covering a total area of 2 m^2 were placed under one tree with a canopy of 42 m^2 in the autumn. Each trap consisted of a vertical cone of netting opening by a small aperture into a collecting cylinder. The base of the trap was attached to a circular band of galvanized iron some 6 in. deep, which was buried in the soil, and the top of the trap was suspended from a post to make the apparatus rigid.

The number of female moths collected in these traps was compared with the number of moths caught in the grease band on this tree. It was found that the yield per m^2 of canopy-covered ground was 70 % higher in the traps than in the grease band. This difference may have been due either to sampling errors (only five out of 20 moths in the ground traps were males, instead of the expected 1 : 1 ratio) or to the exclusion of ground predators. However, it suggests that the number of female moths caught in the grease bands may not be as high as the actual population of these moths in the habitat. The average number of female moths ascending the trees reached a peak on 9 December in both plantations, and 45 % of the total number trapped on the trees were caught in the period 7–12 December. The first moths appeared in the first week of November, and the last at the end of February, but most of the population was trapped in early December.

The total number of female winter moths trapped in Nagshead averaged 443 individuals per tree, and in Barnhill 350 per tree. (It is interesting to note that the moth population per tree in the nest-boxed area was so much higher than in the control area, although the titmouse population in the breeding season was twice as great in Nagshead as in Barnhill.) The estimates of the total female moth populations per acre of woodland, therefore, were 27 900 individuals in Nagshead and 10 900 in Barnhill. Actually, the moth population in Nagshead is a little higher than this figure, for no account has been taken of shrubs in this area.

The average number of eggs in a sample of female moths trapped before laying had started was about 200 eggs per moth, so that for 1951 there was a potential population of over five million *O. brumata* larvae per acre of woodland in Nagshead, and over two million per acre in Barnhill. The subsequent larval populations were, in fact, roughly one-tenth of these numbers, and the high mortality rate between the two stages raises the possibility of predation by titmice on the adult moths.

(*e*) *Effect of predation by titmice on the adult winter moth population*

The following calculations are based largely on approximations, but they give some indication of the possible effect of predation on the moths. The number of adult winter moths in the gizzards of titmice taken in December from this area averaged 21 per great tit, 17 per blue tit, 9 per coal tit and 16 per marsh tit. The fragments of moths in the gizzard contents have been taken to represent the number eaten during the 2 h previous to the death of the bird. The rate of digestion in wild titmice has not been measured, but this figure has been computed from data given by Bryant (1914) and Collinge (1927) for the digestion-rate in captive passerine birds, and from data derived from a comparison of gizzard contents with the average feeding-rate of nestling titmice. The average time between awakening and roosting at this time of the year is $8\frac{1}{2}$ h, therefore each titmouse may take some 65 moths per day.

It was not possible to count the titmouse population in this large area of woodland in December but a rough guide may be obtained from the adult population in the following April. At the start of the breeding season this was about three titmice per acre in Nagshead and one per acre in Barnhill. These figures do not take into account the considerable mortality which takes place from December to April, but the decrease is counteracted by the movement of birds into the area in the spring (Kluijver 1951). On a basis of these rough figures the proportion of the total moth population which might have been eaten by titmice during the period when most of the moths emerged was about 10% in each plantation. However, where it was possible to determine the sex of the moths in the gizzards, it was found that females greatly predominated, nearly all being females in the blue and coal tits, and 70% in the great tit. Hence the predation rate on the females may have been about 20%.

Other variables enter into the calculation of the predation rate. Thus, as shown in Fig. 4, a hard frost stops the movement of the moths, while after a rise in the temperature there is a sudden flush in the numbers of moths on the trees. Hence, the number of moths eaten by titmice may well be higher in a mild December, when there is a steady stream of moths each day, than in a period with intermittent hard frosts when the number of moths fluctuates widely from day to day. A continuous snow cover at this time may cause the birds to move out of the area (Gibb 1954*b*) and so affect the amount of predation. Another variable is the abundance of alternative food. In December 1950 there was a heavy beech-mast crop and titmice spent much time in feeding round the beeches, whereas in December 1948 and 1949 they fed mainly in the oaks.

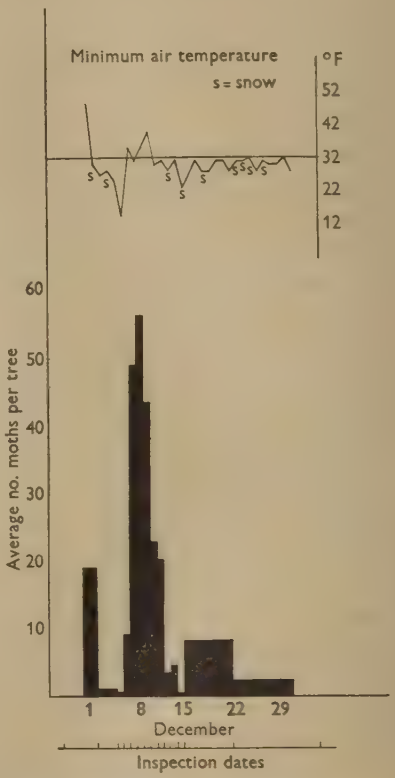

Fig. 4. The effect of temperature on the movement of female winter moths.

Although many writers have assumed that birds play an important role in the control of insect populations, very little study has been made of the actual effects of bird predation on the populations of their insect prey. When an insect population increases to plague proportions there can be no correspondingly large increase in the breeding population of birds in the area, as their reproduction rate is low compared with that of the insects. Hence, unless large numbers of birds migrate temporarily into the area, it is unlikely that birds can play an effective role in controlling an established

plague of insects. Tothill (1922), studying predation by birds on the fall webworm (*Hyphantria cunea*), found that only a small proportion of the population was eaten by birds in years when the caterpillars were abundant. Similar results were obtained by Kendeigh (1947) who estimated that 4% of a plague population of the spruce budworm (*Archips fumiferana*) was eaten by birds, although Tothill (1923) found that a much higher proportion was removed by birds, when the budworm population was decreasing after a plague. Kluijver (1933), and R. Carrick (verbal communication) found that tipulid populations were little affected by the predation of starlings, and further evidence is afforded by studies of predation by titmice on defoliating caterpillars at high densities in mixed deciduous woodland made by Hartley & Betts (unpublished).

Tinbergen (1949) studying titmice in Dutch pine woods, found that in a nest-boxed area in the breeding season, the birds removed over one-fifth of the populations of some insect species, when these populations were at a low level. As mentioned before, he also found that, when the density of a prey species increased somewhat, the birds removed a relatively smaller proportion of the population than previously. This agrees with the present data, for the proportion of *O. brumata* larvae in the diet of titmice was smaller in 1950, when the larval population was higher, than in 1951 when this population was lower.

Nicholson (1933) argued on theoretical grounds that if an insect population is controlled by parasites, predation on the host may reduce the parasite population, and eventually lead to an increase of the prey. There is evidence from gizzard analyses that parasitized larvae are eaten by titmice, and by the great tit in particular. These larvae were frequently observed on the ground beneath the trees, and it is suggested that as they are conspicuous, and are sluggish in habit, they might be selected by ground feeding birds.

Present data on predation by titmice on relatively low caterpillar populations have shown that the larval populations were little affected, but predation by the birds in winter on female winter moths might be of some importance in the control of this insect species. There is, at present, little evidence to justify the widely held belief that birds do exert a control over insect populations, but more detailed research into predator-prey relationships, especially at low population densities of the prey, is essential before this assumption can be supported or refuted.

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SUMMARY

1. The possible competition for food between the great and blue tit (*Parus major* and *P. caeruleus*) in oak woodland, and their relationships with the coal and marsh tit (*P. ater* and *P. palustris*), was studied by means of gizzard analyses. There was little similarity in the diets of the great and blue tits, the great tit taking mainly adult insects, especially weevils, while the blue tit fed mainly on scale insects and small larval and pupal forms. The coal tit showed a preference for small free-living insects, and scales. The diet of the marsh tit consisted of adult insects, scales and some larval forms. Spiders formed a small proportion of the diet of all four species. The great and marsh tits fed more on seeds and nuts than did the other species, and oak bud and gall tissue were found in large quantities only in the blue tit.

2. An analysis of the insect food showed that the great tit was largely a ground feeder, except in the breeding season, while the blue tit fed mainly on the oak twigs, buds and leaves. The coal tit showed a preference for insects from trunks and branches, while the marsh tit fed both on the ground and in the canopy. The beaks of the titmice were adapted to the size and types of foods taken by the birds, enabling all four species to feed in the same places without necessarily competing for food.

3. Nestling foods of a brood of great tits and a brood of blue tits reflected the differences in the type and size of foods selected by the adults in the rest of the year. Caterpillars were taken by both species, but pupae extracted from curled leaves formed a much greater proportion of the diet of the blue tits than of the great tits. Adult insects, forming 19% of the great tit nestling food, were not taken for the young by the blue tit. Both species fed spiders, crushed snails and grit to the young. Most of the food items brought to the young blue tits measured under 10 mm, while most of those fed to the great tits measured over this length.

4. Measurements were made of the caterpillar and titmouse populations in a nest-boxed area and an adjoining unboxed control area in 1950 and 1951. The rate of predation by titmice on all defoliating caterpillars in the boxed area was about 1·4% in 1950, 4·8% in 1951, while in the control area it was 0·9% in 1950, 3·2% in 1951. The proportion of the winter moth (*Operophtera brumata*) larvae removed by the titmice in the two years in the nest-boxed area was 0·5% in 1950, 2·6% in 1951, and in the control area 0·3% in 1950, 1·7% in 1951. In both years the caterpillar population was relatively low compared with the 1949 populations. In the winter of 1950–51 it was estimated that the predation rate by titmice on the female winter moths might have been about 20% in both areas. This predation on the moth population may be affected by climatic conditions, and the abundance of alternative food for the birds.

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THE INFLUENCE OF THE PREVAILING WEATHER ON THE NUMBERS OF *MEROMYZA VARIEGATA* MEIGEN (DIPTERA, CHLOROPIDAE) CAUGHT WITH A SWEEPNET

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(With 2 Figures in the Text)

Some of the variance in the numbers of insects caught by sweepnet sampling has been ascribed to the effect of the prevailing weather on insect activity and on the vertical distribution of the population within the vegetation. If the effect of the prevailing weather on both the activity and the vertical distribution is consistent from occasion to occasion, a coefficient could be derived with which it would be possible to correct the sample numbers to standard conditions of at least some of the weather factors. The present work demonstrates the derivation of such a coefficient for the Chloropid fly *Meromyza variegata* Meig. For these experiments a grassland insect was chosen, since such vegetation forms a relatively uniform habitat, and flies of the genus *Meromyza* are the most conspicuous species which occurs in sufficient numbers at the Field Station to be suitable for this work. The largest species *M. variegata* was chosen as it could be conveniently sieved from the large amounts of grass seed which were taken in the sweepnet at the time of the year when the adult insects were available (July–August). *M. variegata* occurs in very large numbers on the five-acre patch of cocksfoot (*Dactylis glomerata* L.) which forms part of the Main Field, and half an acre of this was laid out as an experimental plot.

In deriving this coefficient for *M. variegata*, the assumption has been made that, under constant weather conditions, a standardized method of sweeping will sample a constant proportion of the population. The possibility that behaviour changes other than those induced by the weather may affect this assumption has been ignored, but the probability of differences between the sexes is discussed later. Since the size of the absolute population did vary over the period of the experiment, the changes in numbers associated with the weather will be related to the size of the absolute population at the time of sampling. Therefore the object of the experiment was to relate the numbers of flies caught with a sweepnet to the prevailing weather in a way such as to make possible a forecast of the relative size of the catch which could be expected under different combinations of conditions. The method adopted was to collect samples of the population under measured environmental conditions and to determine the partial regression of the relative size of the catch on each of the weather factors. By expressing the catch as a logarithmic value ($\log n+1$), the antilogarithm of each of the partial regressions gives the multiple by which the population apparently changes for unit change of that weather factor. From such results it was easy to derive a reasonably accurate forecasting coefficient of the effect of different combinations of weather conditions.

METHOD OF SAMPLING

The standard kite type of sweepnet with a strong linen bag was used to collect the samples. From the results given by Carpenter & Ford (1936) it may be inferred that an experienced collector may unconsciously select or reject fruitful parts of the sampling area and therefore some method of preventing this type of bias is necessary. The purposive method of sampling, known as line sampling, is that to which sweeping can be best adapted. This method, in which the sweepstrokes are taken at equal intervals along a line transecting the study area, tends to select a sample catch near to the mean value for the whole area. This tendency is an advantage as the individual variation between sweepstrokes (which would be reflected in fully randomized samples) is not so important, in this experiment, as a good estimate of the differences between the mean size of the populations on different occasions. The interval between sweepstrokes along the line was taken as one pace (30–36 in.), and by walking briskly, sweeping the net across the toes in alternate directions at each pace, a rhythmic movement resulted which minimized the biased selection of the position of any sample. A line of fifty sweepstrokes was used as the standard sample unit.

Since knowledge of the variability of the population density in different parts of the sampling area was not one of the requirements of the work, by taking the line-sample across the major variations of the habitat, minimal variance between the catches taken on different occasions could be expected (Beall 1939). There is, however, the suggestion (De Long 1932) that the direction of the wind compared with the direction of sweeping may affect the number of insects caught. To take both these points into consideration the sample line was divided into two parts, each consisting of twenty-five sweepstrokes, and lying parallel on the experimental plot. Both lines lay across the major variations of the vegetation, and it was hoped that by reversing the direction of sweeping on the second line, the effect of wind direction on the size of the catch would be reduced.

This standardization of the sweeping technique was tested in a pilot experiment by two operators using identical types of sweepnet. For assistance in carrying out this experiment the writer is indebted to Mr I. W. B. Nye of the College research staff. On six occasions from May to July 1952, counts were made of all the Diptera from pairs of ten-stroke sweep samples taken simultaneously by two operators on each of the five experimental plots. The following results were obtained: the mean numbers of flies caught per sample were—Nye 34·4, Hughes 31·1; the least significant interval between these means was 6·8 flies. If, to reduce the importance of two high counts among the thirty made, the geometric means are calculated, the results speak for themselves—Nye 27·5, Hughes 27·0. This standardized sweeping technique (with only one operator) was used throughout the work to give unbiased samples of the *M. variegata* population.

METEOROLOGICAL RECORDS

When considering the effect of the weather on the population, an estimate of the microclimate over the whole of the habitat is required. Owing to the variability of even an apparently uniform plot of grassland, it is inadvisable to rely on the measure-

ments of the microclimate at any one point to give this estimate. The simplest solution to this problem is to determine which climatic factors control the grass microclimate, and to use ordinary meteorological data from a Stephenson Screen, transformed where necessary, as measures of the micro-climate.

As a result of preliminary studies of the micro-climate of grassland, the conditions at any point within the grass layer were regarded as a function of four climatic components: air temperature, rain, wind, solar radiation (the last being considered as a two-component system comprising the intensity and the directional component dependent on the angle of the sun). In these studies I used the available information of the modification of these factors by the vegetation (Geiger 1950) to deduce the microclimate patterns of temperature and relative humidity, produced by their interaction.

Small ($0{\cdot}5 \times 2{\cdot}0$ mm) copper-constantan thermocouples were used to make more or less simultaneous measurements of the air temperature within the grass layer. These measurements were then compared with the prevailing weather a few feet above the vegetation. Such thermocouples give measurements of temperature proportional to the temperatures obtained by a particular insect of similar size under identical conditions (Parry 1951). A small wooden stand was made to hold the thermocouples at various levels within the grass and the measurement within 15 sec of the temperatures at ten different points was made possible by the use of a multiple switch. The instruments used to measure the conditions external to the grass layer were a shielded thermometer, a cup anemometer, and a barrier-layer photometer measuring the vertical component of light intensity, all of which were mounted 2 ft above the top of the grass layer. The photometer reading was used as a simple measure of solar radiation, since its readings were shown to be proportional to the multi-directional total radiation (measured with a spherical actinometer designed and kindly lent by Mr J. W. Siddorn) over short periods of time.

With this apparatus it was possible to show that while over long periods of time the temperature within the grass layer is closely related to the external air temperature, the minor fluctuations from minute to minute are associated with the intensity of solar radiation and the wind speed. These latter relationships can be seen in Fig. 1, which shows an example of temperature fluctuations at three different levels within a grass layer, compared with the prevailing radiation and wind. These measurements taken in May 1953 show that over the summer period solar radiation is strong enough to raise the air temperatures within the grass layer by appreciable amounts. As green vegetation reflects a major proportion of long-wave radiation (Duggar, quoted by Laidlaw 1951), both direct and reflected sunlight raise the air temperatures within the grass. The decrease in temperature apparently associated with the wind speed is probably caused by mixing with the cooler air from outside the grass layer, the amount of mixing at any point being determined by the wind speed at that point. The probable daytime relationship of solar radiation and wind speed within a grass layer is represented diagrammatically in Fig. 2. The intensity of radiation within a grass layer has been shown (Angström 1925) to fall as the distance from the upper surface increases. This fall is slow at first but becomes more rapid as the vegetation thickens near to the ground. Preschke's data (Geiger 1950) show that there is a rapid reduction of wind-

speed below the upper surface of standing wheat, and it is likely that this reduction is typical of all grassland habitats.

While the temperatures within the grass are primarily governed by the temperatures of the soil and the air, wind and radiation changes will cause characteristic irregu-

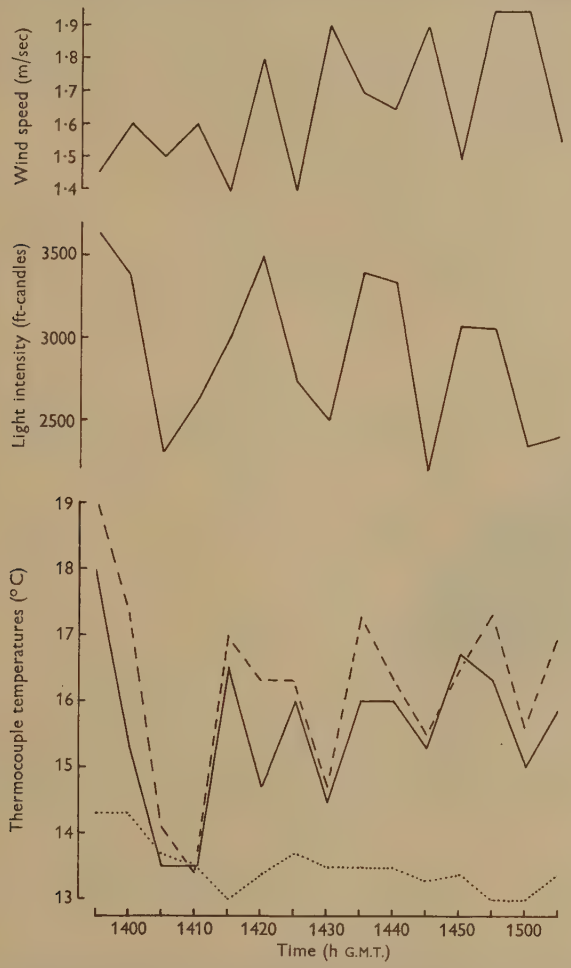

Fig. 1. Temperature fluctuations at three levels within an even stand of grass 14 in. high, compared with the wind speed and light intensity (radiation) measured at 2 ft above the grass; full line—at the top of the grass, pecked line—4 in. below the top of the grass, dotted line—at the base of the grass.

larities on the temperature profile. An example of such a temperature profile is also given in Fig. 2, and shows how above the steep soil–air gradient, the temperatures continue to rise more slowly with the increasing radiation until a critical point is reached where the wind speed becomes antagonistic to a further rise and a reverse gradient occurs. Such profiles seem to be typical of grassland on summer days.

At any one time the maximum temperature level can be seen to depend on the intensity of solar radiation and the wind speed above the grass layer. During the course of a day, however, direct sunlight penetrates different distances into the grass layer. This variable penetration is the result of the changing angle of the sun, being proportional to the sine of the angle of elevation, if the grass is considered as a system of vertical components. The level within the grass down to which primary reflexion will occur will also be governed by the penetration of the sunlight. The radiation gradient within the grass (see Fig. 2) will be related to the sine of the angle of the sun, and thus the level of maximum temperatures will also vary with this quantity.

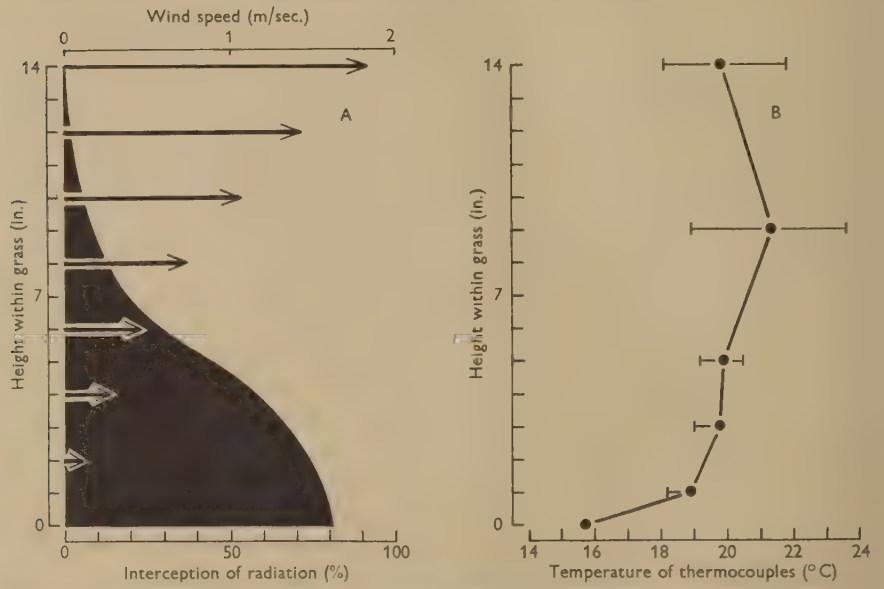

Fig. 2. A. The probable type of wind and radiation relationships within an even stand of grass 14 in. high. B. A typical temperature profile within such grass, measured with small (0·5 × 2·0 mm) copper-constantan thermocouples. The curve is the mean of fifteen taken at 5 min intervals beteeen 1305 and 1420 G.M.T. on 13 May 1953.

Relative humidity was studied in less detail. A lack of suitable recording instruments for this type of work was the primary reason for the deductive approach to this problem, although the broader tolerance shown by many insects towards relative humidity in the field (De Long 1932, Williams 1940, Underhill 1940 and Romney 1945) seems to indicate that a lesser importance may fairly be assigned to this factor. The general relative humidity in the grass was considered in terms of the length of time since the air within the grass layer was saturated. Saturated conditions occur when dew is falling and during rain, and thus the primary humidity factor was taken as the time since dew or rain fell, whichever was the shorter. The end of dew fall was taken to be sunrise. The rate of drying of the grass layer can be considered to be roughly exponential, and thus the time since saturation has been expressed on a logarithmic scale. The rate of drying will be modified by changes of wind speed, solar

radiation and air temperature, while at different times of the day the rate will vary with the penetration of sunlight.

These four factors can thus be seen not only to express the prevailing conditions of wind, radiation, rain and the general level of temperatures, but also to give some measure of the interactions of these factors which produce the microclimate experienced by the insects in different parts of the grass.

As a result of these preliminary studies the following data were determined when the population of *M. variegata* was sampled:

Air temperature	Shielded thermometer 4 ft above the ground, at the site
Wind speed	Cup anemometer 4 ft above the ground, at the site
Total solar radiation	Robitzsch actinometer 200 yd from the site
Sine of the angle of elevation of the sun	Time of day and the Nautical Almanack
Log_{10} (hours since saturation)	Dines tilting-syphon recording rain gauge, 200 yd from the site; and the Nautical Almanack

The basic data are given in full in Table 1.

THE METHOD OF RELATING THE CATCH OF *MEROMYZA VARIEGATA* TO THE PREVAILING WEATHER

The object of this investigation was to determine the relation between the prevailing weather and the variations of the numbers of *M. variegata* about a mean value. As the sampling extended over the period of several weeks, actual changes in the population caused by the emergence and death of the insects resulted in a change in the mean numbers caught. This change was not associated with the action of the weather conditions on the insect behaviour and therefore tended to mask that effect. To give a constant mean value to the data, these were transformed by estimating the long-term trend in the size of the population and expressing the catch as a deviation from this calculated expectation. Several methods of determining the long-term trend in such data have been suggested (Williams 1940). As *M. variegata* has a well-defined single adult generation per year, it was found that the population trend could most easily be estimated by fitting a simple curve to the catch data.

The rectangular distribution of sample counts over the period of the experiments (Table 1) seemed to indicate that the life of the adults was long compared with the time taken for the population to emerge. This hypothesis was supported by the increasing rarity of newly emerged adults (which have a characteristic green colour turning to the normal yellow within a few days) after the first fortnight of the adult generation. This evidence suggests that the population trend as reflected in the samples can be regarded as the ordinate of the integrated emergence curve less that of the mortality curve.

The sample counts of the population remained at more or less the same level during the second half of July, and it was decided to fit the data up to the end of the month with a curve based on the integration of a hypothetical emergence curve. Since this period covers the majority of the sampling days the remainder were not used in the calculations. The first hypothesis tested was that the emergence curve could be

regarded as a Binomial distribution of emergence about a mean day. By setting this mean day at different distances from the possible start of the emergence, the length of the 'tail' of the intergrated curve is altered. By trial and error a mean of 17 days after the start of the emergence was found to give a 'tail shape' similar to that of the experimental data. A curve based on the integration of the Binomial expectation of

Table 1. *Basic sampling and meteorological data*

Date (1953)	Time (G.M.T.)	Sun shining	Wind (velocity m/sec)	Air temperature (° C)	Mean radiation intensity over previous hour (arbitrary units)	Hours since saturation (10 indicates 10 or more)	No. of flies caught	No. of male flies caught	No. of female flies caught
4 July	10.10	–	1·25	21·5	25	6	4	1	3
4 July	11.15	–	0·95	26·5	24	7	2	2	0
4 July	15.45	+	1·05	27·0	19	10	1	1	0
5 July	09.45	+	1·45	29·0	31	6	9	1	8
5 July	10.45	+	1·55	32·5	42	7	5	2	3
5 July	16.45	+	1·50	25·0	25	10	6	2	4
6 July	09.35	–	1·65	19·0	12	1	10	5	5
6 July	12.55	–	1·40	20·5	12	4	15	10	5
6 July	15.45	–	1·75	26·0	27	7	6	6	0
7 July	09.35	–	2·10	19·5	21	6	3	2	1
7 July	11.55	–	2·20	19·0	8	8	10	2	8
7 July	14.45	–	2·10	18·5	9	10	4	3	1
8 July	08.45	+	2·10	18·5	21	5	12	4	8
8 July	11.15	+	1·85	20·5	28	7	17	11	6
8 July	15.00	+	2·15	25·5	33	10	16	10	6
9 July	09.25	+	1·85	18·5	23	7	13	10	3
10 July	14.51	+	2·60	24·0	39	10	39	24	15
10 July	15.55	+	2·50	23·5	31	10	16	12	4
11 July	09.40	–	1·20	18·5	3	6	47	28	19
11 July	11.15	+	2·50	20·5	30	7	15	9	6
11 July	14.40	–	2·10	18·5	31	10	59	28	31
13 July	09.35	–	2·20	14·5	10	1	48	29	19
13 July	17.50	+	2·15	17·5	19	3	66	40	26
14 July	09.50	–	1·20	17·5	20	6	34	18	16
14 July	13.35	+	2·45	16·0	27	1	34	18	16
14 July	18.25	+	1·15	17·0	12	5	62	35	27
15 July	09.05	+	2·00	18·5	29	5	62	46	16
15 July	10.40	+	2·05	22·0	39	7	46	27	19
16 July	09.31	–	2·60	17·5	13	6	47	28	19
16 July	12.50	–	2·35	18·0	23	1	41	26	15
16 July	17.55	–	1·30	15·5	6	4	85	50	35
17 July	07.30	+	2·35	16·5	15	4	30	18	12
17 July	13.00	+	2·70	19·5	44	2	32	17	15
18 July	09.25	+	2·20	17·0	29	2	64	44	20
18 July	12.55	+	2·00	23·0	23	6	57	28	29
19 July	09.35	+	2·15	19·0	33	6	48	32	16
19 July	11.15	+	2·90	21·0	39	7	60	36	24
20 July	10.20	+	1·90	20·5	27	7	63	33	30
20 July	16.20	+	2·15	23·0	29	10	51	34	17
21 July	09.15	–	1·60	19·5	15	5	67	37	30
21 July	13.45	–	1·40	20·0	12	10	85	63	22
22 July	12.47	+	1·80	19·5	43	1	77	49	26
23 July	08.45	–	1·55	15·5	13	3	98	63	35
23 July	13.05	+	1·45	20·5	28	1	103	54	49
24 July	10.20	+	1·90	18·5	34	6	81	40	41
24 July	13.40	+	2·50	21·5	36	10	51	36	15
25 July	13.40	+	1·95	25·0	40	10	47	22	25
26 July	11.05	+	2·50	16·5	32	1	51	32	19
27 July	11.05	–	2·10	17·5	26	7	35	14	21
27 July	15.25	–	0·95	16·5	22	3	79	50	29
28 July	08.55	+	1·40	18·5	27	5	95	53	42
28 July	12.50	–	2·25	20·5	41	2	74	46	28
29 July	08.40	–	1·05	16·5	6	5	72	51	21
29 July	16.10	–	1·05	16·0	15	1	105	51	54
30 July	11.55	+	1·85	17·5	40	1	75	39	36
10 Aug.	13.10	+	2·50	26·5	44	9	63	38	25
11 Aug.	09.00	+	1·85	22·5	19	5	61	31	30
12 Aug.	13.30	+	2·15	32·0	34	9	50	20	30
13 Aug.	16.35	+	1·55	22·3	18	10	49	24	25
14 Aug.	09.50	+	1·00	17·5	26	6	31	12	19
15 Aug.	10.40	–	1·60	17·5	7	1	37	21	16
17 Aug.	08.50	+	1·60	17·5	21	5	13	7	6
17 Aug.	17.00	+	1·40	19·0	17	10	25	12	13
18 Aug.	07.45	+	1·35	16·5	6	2	7	5	2
19 Aug.	13.15	+	1·60	23·7	32	9	8	5	3

emergence about this mean day was therefore used as a measure of the population trend.

If the insect's behaviour is affected by all the weather factors measured, the catch of *M. variegata* will be simultaneously related to the five weather variables and the population trend. The necessity for considering the correlation of the catch with the conjoint effect of the weather factors has been stressed (Williams 1940), since not to do so would bias the estimates of such correlations. For the same reason it was thought desirable to include the population trend as an extra variable in such a multiple correlation. As has been noted in the introduction, the catches have been expressed on a logarithmic scale and therefore the trend variable must also be expressed in such a manner.

During the process of counting the flies were sexed, and thus not only the total numbers of flies but also the numbers of each sex were known. If the assumption is made that the sex-ratio remains constant over the period when the samples were taken, the numbers of the separate sexes will be related to the same six variables as the total catch. By using the 'inverse matrix' method of estimating the multiple correlations (Fisher 1946), the association of these six variables with all three dependent variables (i.e. total numbers and the numbers of each of the sexes) to give interesting information on the comparative behaviour of the sexes towards the weather, can be computed with only little increase in the work of calculation.

Table 2. *The regression coefficients (with fiducial limits) of the log. catch of* Meromyza variegata *on the trend and weather variables*

	Total	Males	Females
Trend	$+1{\cdot}2336 \pm 0{\cdot}1713$	$+1{\cdot}2504 \pm 0{\cdot}1772$	$+1{\cdot}0927 \pm 0{\cdot}2440$
Wind speed	$-0{\cdot}1774 \pm 0{\cdot}1004$	$-0{\cdot}1789 \pm 0{\cdot}1038$	$-0{\cdot}1995 \pm 0{\cdot}1430$
Time since saturation	$-0{\cdot}0815 \pm 0{\cdot}1426$	$-0{\cdot}0660 \pm 0{\cdot}1477$	$-0{\cdot}1065 \pm 0{\cdot}2030$
Air temperature	$+0{\cdot}0048 \pm 0{\cdot}0202$	$+0{\cdot}0046 \pm 0{\cdot}0211$	$-0{\cdot}0006 \pm 0{\cdot}0290$
Radiation intensity	$+0{\cdot}0010 \pm 0{\cdot}0059$	$+0{\cdot}0002 \pm 0{\cdot}0061$	$+0{\cdot}0024 \pm 0{\cdot}0084$
Radiation, penetration	$-0{\cdot}0367 \pm 0{\cdot}2424$	$-0{\cdot}0359 \pm 0{\cdot}2507$	$-0{\cdot}0611 \pm 0{\cdot}3446$
Ascribable variance (%)	89·48	89·02	78·02
Variance ascribable to trend alone (%)	74·37	73·11	69·79

These associations are given in full in Table 2, in which it can be seen that only the population trend and wind speed account for significant parts of the total variation. Comparing the estimate of the amount of variance which can be ascribed to the trend alone, with that ascribable to all six variables, the distinct reduction in the unaccounted variance amounts to nearly 60% in both the total catch and the male catch data. In the female catch data, however, the unaccounted variance is reduced by less than 30%.

While the weather variables, apart from the wind speed, do not account for a significant part of the total variance, they play an important role in forecasting the proportion of the mean catch which can be expected under any specific set of weather conditions. With the catch data transformed on a logarithmic scale this forecasting is made relatively simple, because if on the occasion of sampling the deviations of the six factors from their means are multiplied by their respective regression coefficients,

the antilogarithm of the sum of products indicates the proportion of the mean catch which can be expected under those conditions.

This forecast can only be applied to the original experimental data since the trend variable of that particular population is included, but it is clear that by discarding the population trend, the weather regressions used alone will give a coefficient descriptive of the effect of the prevailing weather independent of the size of the population concerned. The number of flies which could be expected in the samples if the weather conditions were always constant (at levels represented by the mean conditions of the original experiment) may be estimated by dividing the combined weather coefficient into the actual sample numbers obtained.

The correction of the sample catches of flies for changes caused by the weather has not yet been attempted to any large extent on the basis of these results. The reason for this is that there are so far no suitable data available except those from which the results were derived. It seems possible, however, that such estimates can be used to show changes in the size of the population largely independent of errors caused by the weather.

DISCUSSION

In using the multiple correlation technique to determine the relation between the variation in the size of the catch and the weather factors, two important assumptions have been made. First, the effect of all the factors acting conjointly has been assumed to be the same as that produced by summing the effects of each of the factors as if it were acting alone, i.e. that no one factor is acting to limit the effect of any of the others. If a limiting factor does occur it may disguise the significance of others when the multiple correlation technique is used. The second assumption of the present calculations is that there is a linear (or simple curve, when using log. catch) relationship between the variation in the size of the catch and each of the weather factors. Therefore unless second, or higher powers of the variables are used in the calculation, no account can be taken of optimum catch conditions which occur within the experimental range of values attained by the factors. The non-linear relationship of a factor may therefore render the effect statistically insignificant if this technique is used.

As noted in the introduction, various authors have ascribed the effect of the weather on the size of the sweepnet catch either to changes in the amount of insect activity caused by the weather or to changes in the position assumed by the population within the vegetation under different weather conditions. Changes in the vertical position of the population will be reflected in the numbers caught because the sweepnet sample is only taken from the upper layers of the grass. In the present analysis, each of these alternatives or a combination of both, may equally be applied to interpret the effect of some of the factors used. Wind speed is a factor of this type. Individuals of *M. variegata*, in both the field and the laboratory (wind tunnel), have been observed to cling more tightly to their substratum when exposed to windy conditions. Such an increased hold on the vegetation may account for the reduction in the numbers swept off the grass when the wind is strong. Alternatively, the insects may actively seek shelter from the wind amongst the lower vegetation or on the ground (De Long 1932), or be blown off the higher parts of the grass, from which the sweepnet sample is

taken. Some corroboration for the latter explanation can be inferred from the fact that no increase in the catch occurs if each sweepstroke is replaced by brisk multiple sweeping at each sampling point (Romney 1945). The disturbance caused by the repeated sweeping of the same vegetation would seem sufficient to dislodge even a tightly clinging insect.

There are three possible interpretations of the influence of the period elapsing since the saturation of the air amongst the grass. The numbers of flies may increase after the grass has been saturated because of the activity induced by the high humidity. Alternatively, the insect may be trying to leave the saturated conditions within the grass (De Long 1932), the bulk of the population moving to the upper surface of the vegetation where the conditions are least humid. A third explanation, which has some foundation in observations made by subjecting flies to a spray of water, is that flies hit by rain drops move to the upper surface of the grass layer to carry out cleaning movements. Further evidence that this association with rain may be the explanation of the general effect is that if the humidity is represented by the time since rain stopped falling, rather than the period since saturation of any type, the log. total catch has a regression on this variable which closely approaches significance and the log. catch of males has a significant ($P = 0{\cdot}05$) regression upon it.

Both the air temperature and the intensity of radiation govern the body temperature of the insects, and it seems most likely that the response to these factors is the increase of activity associated with high temperatures. However, the effect of radiation intensity upon the height of the maximum temperature zone within the grass should also be remembered. The height of this zone depends on the balance between the wind speed and the radiation intensity within the grass (as was pointed out in the section on meteorological records), and an increase of radiation intensity causes the zone to rise. An upward movement of the fly population into the zone of higher temperatures could account for the increase in the catch of flies associated with high radiation. The penetration of sunlight into the grass (coefficient = sine of the angle of elevation of the sun) will also affect the height of the maximum temperature zone and the increase of the catch when the sun is low is probably caused by movements of the population associated with the high level of the maximum temperature zone within the grass.

The regressions, as calculated above, cannot be regarded as numerical measurements of purely behaviour effects, owing to the possibility that the weather, by altering the emergence- and death-rates from day to day, may also be affecting the actual numbers of the population (Johnson 1952). Because of this possibility, detailed observations of the actual behaviour of the insects are necessary before it will be possible to explain accurately the effect of a particular weather factor on the size of the catch. One difficult problem, which needs clarifying before further work is attempted on this subject, is to discover if the number of insects caught in the net is directly related to the amount of activity they display, or if there is an optimum level of activity which gives the best catch with a sweepnet. The writer has made a preliminary attempt to reproduce natural conditions in the laboratory, so that observations of the behaviour of groups of flies under different conditions may be studied. This apparatus will be described in a later paper. So far no elaborate experiments have been attempted, but

pilot observations show that this type of technique may provide a clue to the action of at least some of the factors upon the number of flies caught.

In interpreting the general effect of the weather on the size of the catch, one of the most interesting points is the apparent difference in the effect upon the two sexes. The weather can explain some 30% of the variance in the log. catch of the females which is not accountable to the population trend, compared with some 60% in the case of the males. The behaviour of the females under different weather conditions, as is reflected in the size of the sweep catch, is apparently much more unpredictable. Of the possible reasons for this difference, special female behaviour associated with oviposition seems to be most likely.

The work of De Long (1932) and Romney (1945) has shown that the weather will affect the sweepnet catches of insects other than *M. variegata* in a similar manner. With the smaller insects (but not very small), wind speed seems likely to be always the major weather factor affecting the sweepnet catch, but extremes of any factor may also substantially alter the numbers caught. The similarity of the weather's effect on closely related insects can be seen in the marked reduction in the variance of sample numbers of *M. saltatrix* (L.) which have been corrected with the weather coefficient derived from *M. variegata*, Table 3.

Table 3. *The correction of the sample numbers of* Meromyza saltatrix *with the weather coefficient derived from the* M. variegata *data*

Date	Actual catch *M. saltatrix*	Weather coefficient *M. variegata*	Corrected sample catch
8 July 1952	24	0·41	59
10 July 1952	26	0·81	32
10 July 1952	35	0·58	60
11 July 1952	30	0·50	60
14 July 1952	15	0·40	38
14 July 1952	39	0·44	89
15 July 1952	24	0·60	40
17 July 1952	15	0·39	37
17 July 1952	55	0·66	83
18 July 1952	56	0·78	72
21 July 1952	84	1·17	72
21 July 1952	92	1·27	72

The existence of a further portion of the residual variance which is potentially ascribable to other climatic factors by the use of a method of this type, remains a matter for speculation. Throughout the work, and especially in the few preliminary observations on the behaviour of the flies, there have been clear indications that marked changes in activity are caused by rapid variations of the prevailing conditions. In the field, such activity changes may alter the catch by considerable amounts, especially in the highly variable conditions of an English summer. There is also a clear possibility that some hitherto unmeasured factor may account for a large portion of the unaccounted variability in the sample catches.

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SUMMARY

1. A study was made of the relative size of catches of the fly *Meromyza variegata* Meig., obtained by sweeping grass under different weather conditions during the summer of 1953.

2. The microclimate of the grass is shown to be directly related to the prevailing conditions of air temperature, wind, rain, and solar radiation, as modified by the structure of the vegetation.

3. A statistical analysis of the results showed that apart from actual changes in the size of the population, an increase of wind speed is clearly associated with a reduction in the number of flies caught.

4. The occasionally discrepant sizes of the catch of both this fly and the closely related *M. saltatrix* (L.) could be explained once the dependence of the size of catch on the weather conditions had been ascertained. Although each factor had not necessarily a significant influence on the catch size in itself, the multiple regression of the catch size on all the measured factors gave predicted catches in good agreement with the observed values.

5. The probable mechanisms of the effect of each weather factor on the catch size are discussed.

6. An apparently greater reaction of the male flies to differing weather conditions is discussed.

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FOOD COLLECTION BY A SCOTTISH ANT COMMUNITY

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(With 2 Figures in the Text)

INTRODUCTION

This is an account of the foraging behaviour of the four-species ant population that is characteristic of acidic grassland and moorland in west Scotland. Emphasis is not on what is collected or when it is collected, but on intra-species relations during its collection. The four species are: *Formica fusca* L.,* *Myrmica scabrinodis* Nyl., *M. rubra* L. and *Leptothorax acervorum* F. The community thus comprises a comparatively primitive Formicid and three comparatively primitive Myrmicids, all of wide distribution in temperate regions.

Works on ant foraging and interrelations are now numerous, and at least three authors have written about the same or related species as the above: Pickles (1935, 1936, 1937 and 1938) about the first three species in two communities in England; Morisita (1939*a*, 1941) about *Formica fusca japonica* Motschulsky in its relations with other Japanese ants; and Talbot (1945) about the related *Myrmica schenki emeryana* Forel in Ohio, U.S.A.

FEEDING METHODS

In feeding, these ants follow the common generalized pattern by combining hunting with the collection of honey-dew from Homoptera which are in varying degrees farmed. These Homoptera were principally aphides; some hypogaeic, feeding on grass rhizomes (especially *Agrostis* spp.): others supergaeic, feeding for the most part on the shoots of *Gallium hercynium* Weigel and *Succisa pratensis* Moench. On the latter plant the aphides were situated on the bases of radical leaves and were covered with a more or less complete earthen cover constructed by the ants.

In a quadrat $1{\cdot}8 \times 2{\cdot}1$ m containing two nests of *Myrmica rubra* and two of *M. scabrinodis* every plant was mapped and examined for aphides and ants above the soil surface. Aphid clusters were found on 29 out of 169 plants of *Succisa pratensis* and on one plant of *Luzula campestris* (L.) DC. All groups had attendant ants which were in all cases of either one or the other species. The degree of association was thus maximal, and probably as far as the ant species were concerned monopolistic (experimental evidence on this point will follow). Of the 30 groups, 15 were tended by *scabrinodis* and 15 by *rubra*, and it is apparent more especially with the latter species that they cluster round the nests (Fig. 1).

* According to Dr Yarrow, British Museum (Nat. Hist.), this species is better referred to as *F. lemani* Bondroit.

Although hardly necessary, it is possible to apply a simple statistical test which demonstrates that this is not likely to be a chance arrangement. A non-inflecting enveloping curve can be drawn round each of the four nests in such a way as to enclose all the associated honey-dew sources. These envelopes include some of the free plants too, but they are in a much smaller proportion inside these areas than in the quadrat as a whole. Thus, altogether, the four envelopes covered one-fifth of the area, and yet 27 out of a total of 37 *Succisa pratensis* plants were occupied. If a random

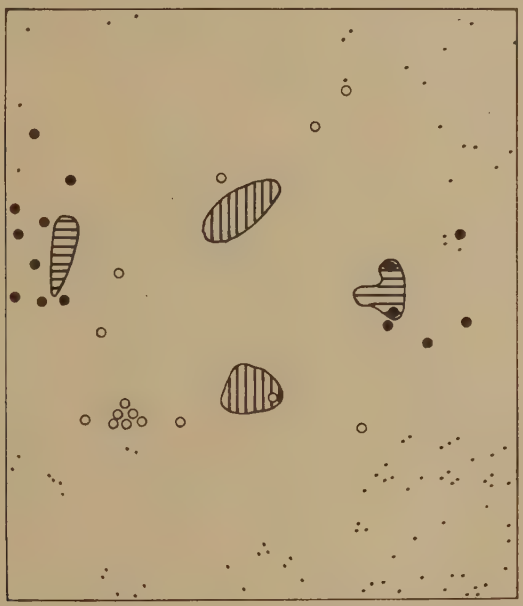

Fig. 1. An area (1·8 m by 2·1 m) with two nests of *Myrmica rubra* (horizontal hatching) and two of *M. scabrinodis* (vertical hatching), in which all the plants of *Succisa pratensis* have been marked (dots and circles). Those with aphides and ants in attendance have been shown as circles, white if tended by *scabrinodis*, and black if tended by *rubra*.

distribution of such occupied plants existed over the whole area 7·7 would be expected inside the envelopes; and so, using the χ^2 test with one degree of freedom, a value of 48·4 ($P < 0{\cdot}001$) is obtained. This would be relevant even if those plants used by the two species of ant were mixed over the whole of the enveloped areas, which of course they were not, each envelope containing the same species of ant as the nest itself. Thus these observations suggest strongly that the ants place the aphides on plants near to their nest. As plants were superabundant, in some cases free zones occurred between the areas enveloping occupied plants.

This section is not primarily concerned with the distribution of hunting foragers but it is interesting to add that these went well beyond the honey-dew areas. Thus the *rubra* nest on the west side hunted principally to the west and that on the east side principally to the east. The westerly colony had a nest of area 0·018 m² enclosed in a honey-dew area of 0·102 m², which in turn lay within a hunting area of 2·32 m²,

and the easterly colony gave the corresponding values: 0·023, 0·139 and 2·69 m^2; and so, in both cases the honey-dew area was five to six times the nest area, and the hunting area about 120 times the nest area.

REACTIONS AT SUGAR SOURCES

Syrup was supplied from a cotton wick dipping into a reservoir that was itself sunk below soil level and inaccessible. About 1·5 cm of wick was exposed. This if placed near to a nest would soon be covered with ants, as a result quite clearly of some recruitment process rather than a chance accumulation of foragers. However, the attendance after quickly reaching a maximum would fall to a steady few after one or two days—presumably through satiation of the colony.

(*a*) *Interspecies relations*

When these sources were placed in areas inhabited by all four species, the result varied with the position. If in a slightly frequented area, the visitors would be casual and of all species and so infrequent as to yield few contacts. If nearer a group of nests, one or other usually monopolized the source. This was usually the nearest, for, except near large nests of *Formica fusca*, whichever species occupied the source first, kept it.

The maintenance of a monopoly does not necessitate any hostility: the members of the occupying species behave confidently, coming and going regularly and filling their crops rapidly; other individuals (of whatever species) behave cautiously and nervously, recoiling rapidly if their extended antennae touch an owner. *F. fusca*, in particular, is excitable and often falls to the ground in its effort to escape. Thus the fact of occupation is enough to prevent the solitary foragers of other species and other colonies of the same species from getting to the source. Occupation produces a change in individual behaviour as in vertebrates from excitable nervous curiosity to self-confidence. Pickles (1936) has noted this change in *F. fusca*; it reacted timorously to workers of *Myrmica rubra* when they met in 'the field', but with immediate aggression when in its nest territory (the *rubra* being there by accident). Morisita (1941), too, has noted the change in *fusca* behaviour when they lose monopoly of an aphis-bearing twig.

The absence of ownership behaviour is well illustrated by the following example. A standard wick source was modified so that by means of a bridge of wire netting the top could be reached from above as well as by climbing up the wick from below. *M. rubra* workers came up from below and fed at the base of the wick, whilst *fusca* workers came over the wire bridge and fed at the top. The foragers were so intent on feeding that they rarely met, although as little as 1 cm divided the nearest, and this situation remained stable. When a contact did occur, caused by a *rubra* wandering about, the pair grappled and fell to the ground usually without disturbing the rest. This perfect stratification of feeding has in fact been found to be more general (albeit partial) and will be considered in detail in a later section: *fusca* climb up vegetation more than the Myrmicae and this habit applied to the trap situation resulted in their approaching the source from above and so avoiding the *rubra*.

Formica fusca may monopolize sources as far as 2·5 m from their nests, a much greater distance than the equivalent value of 1 m for the Myrmicae. It may monopo-

lize them even when *Myrmica* nests are nearer, apparently as a result of their greater foraging range, which in turn is facilitated by the larger size and quicker movement of their workers. These have been seen up to 3·3 m from their nest, compared with 1·3 m for *rubra* and 1·2 m for *scabrinodis*. Pickles (1935, 1936) quotes the corresponding figures: 7·9, 3·1 and 6·1 m respectively, all larger but showing *fusca* ranging farther than the others. In North America the related *M. schenki emeryana* Forel seems to have a range comparable with the Scottish species of the genus, for Talbot (1945) mentions 'a yard or two'. The much smaller workers of *Leptothorax acervorum* have been seen to forage up to 3 m from their nests, so that the distance travelled is by no means size-correlated.

This last species has never been seen to monopolize a source. Their workers are present in the communities in small numbers and usually nest near to other forms in inaccessible crevices or holes in hard wood. They are adept at infiltration and successfully avoid recognition even on crowded wicks. Their 'peaceable and gentle disposition' (Donisthorpe 1927) is well known to myrmecologists.

Near *fusca* nests changes of monopoly from one of the Myrmicae to *fusca* may occur if these find the source first. The process takes place as follows: during the midday period in warm sunny weather the number of *fusca* near the wick increases; they behave in a very excitable manner thrusting on to it and then moving off as a *Myrmica* worker approaches; this continual approach and retraction soon disturbs the *Myrmica* workers so much that they cease feeding, and run quickly over the wick, with jaws open, searching aggressively. As more *fusca* workers gather they come to outnumber the Myrmicae and these in their efforts to chase and capture *fusca* often drop to the ground. Soon the *fusca* workers find the wick clear for some moments at a time and they settle on, start feeding and so gain control. This sort of mild aggression contrasts sharply with the behaviour of higher ants as, for example, *Iridomyrmex humulis*, which is fearless, aggressive, agile, able to forage in column and has remarkable powers of recruitment (Haskins 1945; Goetsch 1952). In the community studied success depends less on pugnacity than on the ability to find food quickly and bring enough workers to cover the source before another group finds it. Thus only small sources near to nests can be effectively monopolized, even *fusca* giving a poor performance when compared with the distance over which higher ants can achieve control. Thus one of the principal lines of evolution in ants has been towards the development of larger colonies of smaller workers with more effective group behaviour. By these means a better searching power is obtained, and a quicker and more effective monopoly of larger and larger food objects. In addition, the smaller size of individuals both absolutely and relative to colony size makes their expenditure a less serious matter and they can advantageously be equipped with unbridled ferocity and complete fearlessness.

The observations of other workers confirm those that have been made here. Thus Pickles (1935) did not note monopoly of populations of aphides on *Chamaenerion angustifolium* (L.) Scop. by *Formica fusca*, *Lasius niger* L. or *Myrmica scabrinodis*, but this plant offers a far larger feeding area. Morisita (1939*b*, 1941), on the other hand, noted monopoly of aphides on twigs by *Formica fusca japonica*. From these they were displaced by *Pristomyrmex pungens* Mayr which showed a stronger group behaviour;

and they thieved from aphides guarded by *Lasius niger* and *Crematogaster sordidula osakensis* Forel. In this Japanese community they were evidently less successful in competition with the other species than in the Scottish community. Morisita has also recorded competition between *Tetramorium caespitum* L. and *Lasius niger*, the former successfully replacing the latter. No instance of a diurnal change in power such as he showed to occur between *L. niger* and *Pristomyrmex pungens* has been discovered.

Talbot (1943) studied the ant *Prenolepis imparis* Say which feeds in autumn largely on rotten fruit. Each fruit they guard against *Lasius alienus americanus* Emery and *Myrmica schenki emeryana* Forel and wasps, driving them off by 'hostile tapping of the antennae'. It is not quite certain whether it was this behaviour which forced *Lasius* and *Myrmica* to eat small insects captured on the ground or whether they did it from preference.

(*b*) *Intraspecies relations*

Individuals of the same species but different colonies can only be distinguished by the nest to which they return. When they are laden, however, they usually return directly as did *M. emeryana* (Talbot 1945). Indeed it is only in the primitive Ponerid genera that this behaviour is lacking (Haskins & Haskins 1950), although there is present a tendency to return fairly soon afterwards by an indirect route. Chance contacts by foragers in the field do not in all probability allow time for recognition, an avoiding reaction being invariably given. On a sugar source, however, an incoming worker has plenty of opportunity to examine those already feeding. They may then remain quiescent and join the feeding group, or retreat rapidly after having merely touched the abdomen of the feeder with their antennae, or act aggressively.

In communities of *M. rubra macrogyna* (Brian & Brian 1949),* the approaching ant, if it detects that the examined feeder is allocolonial, behaves aggressively. If its approach is incautious, the feeder turns round (they usually climb up the wick and start feeding abdomen downwards) and grapples, and the pair fall to the ground and break. On the other hand, the incomer may approach slowly, and examine the abdomen of the feeder carefully without disturbing it; then it grips it by the pedicel (with the mandibles) and lifts it up. In this grip the lifted ant invariably remains quiescent, and is carried right back to the nest of the incomer. Sometimes under circumstances when a perfect grip is not obtained, other ants may become involved, and a group of three or four workers, composed of individuals from both nests, may struggle backwards and forwards along a line between the nest and the source (no perceptible track is formed). Mortality does not occur in the field, but those ants that are successfully dragged into the opposing nest will probably be dismembered. Hence the outcome of these struggles should favour the colony that can bring most workers to the site; that is, it will be related to colony size, proximity and recruitment ability.

Talbot (1945) has described a battle perhaps of this nature between workers from colonies of *Prenolepis imparis* Say. These two colonies came into conflict over a pear, but the fight did not take place on this, but in the trackways, groups of workers struggling and gripping and pulling. It seems highly probable that the object here,

* Following a decision by The International Commission on Zoological Nomenclature at Paris (1948), this now becomes a subspecies.

too, was to pull to the opposing nest. Forel (1928) who took an especial interest in ant fighting describes an artificially initiated fight between groups of *Formica pratensis* Retz. in which chains of workers developed, formed of individuals pulling in opposing directions. He also notes natural battles between colonies of *Tetramorium caespitum* which ranged from mere games of pulling with mandibles to lethal fights involving the use of stings. The cause of this variation in intensity is unknown. Headley (1941) has described similar fighting between colonies of *Lasius alienus americanus* Emery.

HUNTING DISTRIBUTION

(*a*) *Method*

With isolated nests it is often possible to study distribution by directly recording the position of each forager. As in the case of *Myrmica rubra* which has been principally studied, rarely more than 20 are out at one time;* a distribution is only arrived at by repeated visits. Even though time trends may thus be included, these do not prevent the appearance of characteristic patterns.

Where colonies are dense or where the herb layer is so thick as to make detection of hunters unreliable and certainly biased, the technique used by Talbot (1943) was employed. Suitable prey are distributed evenly over the whole area, and as each is located and picked up by the foragers, these can be clearly seen making towards their nest. The most suitable prey were found to be the puparia of *Drosophila funebris* Fab. These are collected from laboratory cultures, washed, surface dried and powdered with aluminium. They are distributed by shaking through a gauze and make very conspicuous silvered objects when held in ant jaws. As a variant, adults of *D. melanogaster* crushed just enough to make them immobile were used.

The best results were always obtained in the morning and, in all those instances to be described, the period of observation has been limited to half an hour. By repeated daily observations and continual superposition of records, patterns have emerged. After plotting the distribution on a map, the area was divided into eight sectors centred on the nest, and described from the north to nest radius, clockwise, 1, 2, 3, ..., 8.

In cases where whole areas with many nests are being studied, the problem of what is a nest and what is merely another nest entrance often arises (cf. Headley 1941), for on desirable sites like rotting tree stumps nests can occur within 20 or 30 cm and equally a single nest can have several outlets often as far apart. Thus as tests of affinity under field conditions are not reliable with these small-colony species, cultures of workers and brood from all the sites have been made in the laboratory in duplicate. After two days in which to settle down, single workers were transferred from culture to culture and reactions noted. This transfer test applied between duplicates gives a control reaction. In cases where the entering ant is accepted there is, nevertheless, always interest in the new arrival. If it behaves excitedly, running about and avoiding contact, the nest-ants can be seen reaching out into its track with their antennae, and it is usually soon lost and unidentifiable in the nest group. Should it enter quietly it is examined and licked carefully by a succession of workers, each staying about a minute. On the other hand, under conditions of hostility, the entering

* Compare with the 25–50 that Talbot estimates for *M. emeryana*.

individual wanders about until it meets a nest-ant when both instantly become rigid, the inmate with its mandibles apart; other ants then approach and adopt the same position. A slight jerky movement, even from an inmate, can release a storm of aggression directed towards itself and perhaps lasting only a few seconds until it is identified. After some minutes of this tense inaction an inmate suddenly jerks forwards and captures the added worker by the pedicel, and in such a way it is carried prone and motionless to the rubbish heap. If this neat grip is missed, the worker is usually held by its appendages by a number of the inmates which may break some off and throw the dismembered body on the rubbish heap. Those that succeed in reaching the heap without undue damage being done to them may, under natural conditions, escape and return to their home—as in the battles for sugar sources already described. Perhaps they are removed from the battlefield long enough to decide the fate of the source; if so, a remarkably curious method of reducing mortality and of converting battles into games exists.

These two types of reaction, the inquisitive and the hostile, are distinct enough provided the tests are not delayed beyond the fourth day in the laboratory, and enable a satisfactory identification of colonies.

(*b*) *Isolated nests*

Three examples of *Myrmica rubra* distribution will be given: two studied by direct plotting and one by baiting.

Example 1. The nest was in a rotting stump in a small gap in a Larch plantation with trees about 9 m high. The ground was only sparsely covered with herbs, being for the most part a simple carpet of larch needles. Two larch trees were within range, one 1·8 m from the nest (in sector 2), and the other 1·6 m from the nest (in sector 7). These were climbed by the ants in search of honey-dew from aphides on the shoots. The final distribution was, in sectors 1 to 8 respectively: 5, 17, 10, 7, 7, 8, 24 and 10; thus showing especial abundance in the tree-containing sectors. This is not a random distribution (χ^2 test: $P < 0{\cdot}001$).

As none of the ants recorded in the tree sectors appeared to be going directly to or from the trees (the traffic up the trees was very slight) it was curious that these hunters should be frequenting the adjacent area. Pickles (1935) has, however, noted that ants often went in prevailing directions, which were in some cases clearly associated with food sources such as aphides on *Chamaenerion angustifolium*. Further, Raignier (1952) and Holt (1955) have also shown that *Formica rufa* hunts from trails that lead to trees bearing aphides. The latter worker showed that about 50 % of those that started on a trail left it before it reached a tree. Although no obvious tracks to the trees exist in the case of *Myrmica* there could be no doubt that their direction is known to the ants and quite likely that imperceptible traces exist.

Example 2. This was a nest in grazed acidic grassland against the side of a rock outcrop. The frequencies in sectors 1–8 were as follows: 8, 8, 5, 17, 30, 27, 6, 6, showing a distinct bias ($P < 0{\cdot}001$ by χ^2 with 7 D.F.) towards the south-west. The cause of this was not ascertainable without destruction of the nest. In this case, samples were taken of the distribution four times a day at 3 h intervals, but no diurnal differences in density distribution were detected.

Example 3. This nest lay at the end of a log orientated due east–west in acidic grassland grazed by sheep. It was investigated by the prey-track method and the distribution of a total of 56 tracks in the eight sectors was (in sequence 1 to 8): 4, 1, 6, 9, 2, 25, 1, 8, which deviates from random giving $P < 0{\cdot}001$. The most frequented sector was that lying along the south side of the log, but apart from the fact that here the grass was greener and more closely grazed than elsewhere no direct cause of the concentration could be discovered. Perhaps root aphides were farmed on the grass rhizomes, or perhaps the rotting log material provided a richer fauna amongst which to hunt.

Thus these three examples amply demonstrate that isolated nests show asymmetric foraging distributions. With this feature in mind, it is now possible to consider foraging distributions in dense nesting populations.

(*c*) *Nest groups*

These ants are like sea birds to some extent in that their ideal nest site and ideal feeding requirements are incompatible; they tend to form groups of nests on well drained shortly vegetated and therefore soil-insolation-high areas and from these they forage into surrounding areas of long vegetation (Brian & Brian 1951).

As with the birds, so with the ants. Nest territory is well known to be strictly observed even in the primitive Ponerines (Haskins & Haskins 1950) and a dominance order (more strictly a replacement order, for dominance varies with conditions) has been shown to exist between the ants of this community type (Brian 1952). In the earlier sections of this paper strong indications have been given that small sugar sources that are often distributed in the vicinity of the nest are also monopolized. The question naturally arises: is a larger hunting area monopolized too? A single example suffices to show that this is not the case. An area of ground around two adjacent stumps in a felled woodland subsere was studied. The vicinity of the stumps bore a short vegetation of the moss *Polytrichum* sp. and *Rumex acetosella* L. with short seedlings of *Calluna vulgaris* (L.) Hull and *Chamaenerion angustifolium* (L.) Scop. Around this, a much taller vegetation, over 25 cm high, was composed principally of young birch trees (*Betula* sp.), bramble (*Rubus* sp.), the fern *Dryopteris spinulosa* (Mull.) Watt, as well as grass (*Agrostis* sp.).

Using the baiting technique it was apparent that foraging zones (home ranges) overlapped a good deal both between and within species. This thus confirms the observations of Pickles (1935, 1936) relating to *Formica fusca*, *Myrmica rubra*, *M. scabrinodis* and *Lasius niger* L., and of Talbot (1943) relating to a community of *Prenolepis imparis* Say, *Lasius alienus americanus* Emery and *Myrmica schenki emeryana* Forel, and (1945) a community of *Formica fusca subsericea* Say, *Lasius alienus americanus* Emery and *Myrmica emeryana* Forel.

But although overlap of home-ranges occurs, there is nevertheless a tendency to a dispersion of prevailing foraging areas between colonies of *M. rubra*. The eight sector foraging vectors of each *rubra* colony have been plotted (Fig. 2). When these are considered in relation to the area enclosing all the points at which foragers were ever found, an idea of the hunting range and distribution is obtained. Each vector set is

asymmetrical just as was the case with isolated colonies. The asymmetry cannot therefore be due as might otherwise have been suspected to intercolony interference. And yet the curious fact is that the asymmetrical 'fields' fit together rather (to oversimplify) as the pieces of a jig-saw puzzle so that the whole area is covered. Thus stump *A*, for example, has two *rubra* nests near its entrance (nos. 1 and 2) and yet there are no records of tracks crossing each other's nests: one foraged predominantly to the north, the other to the south and west. The nest on the east of this stump (no. 3) foraged a good deal to the north-east, although it also foraged a good deal in the same

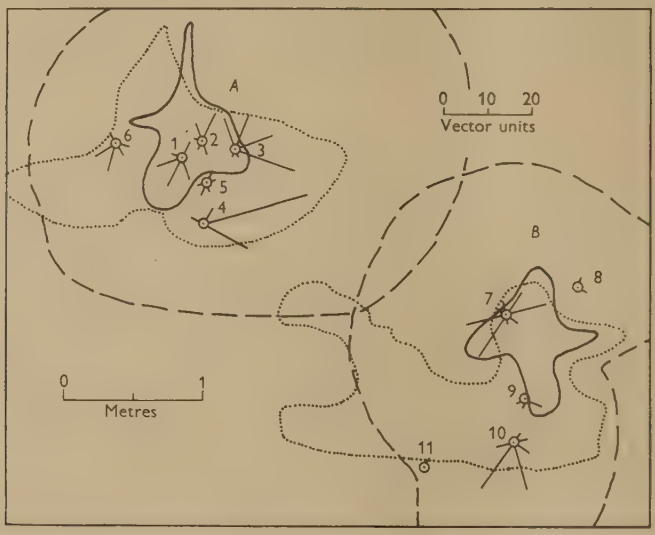

Fig. 2. Foraging vectors of *Myrmica rubra* colonies (numbered 1 to 11) in an area with two rotting tree-stumps (bounded by full lines and lettered *A* and *B*) surrounded by short vegetation less than 25 cm high (bounded by dotted lines) and embedded in an area of taller vegetation (0·25 m to 2 m high). The vector units represent numbers of individual return tracks. A curve (broken line) enveloping all the observed forager positions has been drawn round each stump group of nests.

northerly area as the middle nest. The most southerly *rubra* nest in this stump zone (no. 4) foraged largely to the east, and it was curious to note how bait dropped to the south of this nest went right across it to the stump nests. The home range of nest no. 4 overlapped with that of no. 3 to the extent that a few foragers from the latter walked over the nest. It used the area of long vegetation between the stumps far more than any other nest, even that on the west side of stump *B* which lay just as near. Here again it overlapped the foraging area of nest 3. In the zone of stump *B* it was found that bait dropped to the south almost invariably went into nest 10 which was never observed to forage to the north-west at all. Bait dropped here was taken either to nest 9 or nest 7.

Thus, combining this with the earlier results in this paper, the following general hypothesis may be advanced: that *M. rubra* colonies monopolize sugar sources near to their nest, but often asymmetrically disposed about it, and that hunters forage

from lines (perhaps to them perceptible tracks) connecting the nest with these sources and extrapolated beyond them. As a result of this association of hunting and foraging directions, in dense nest groups there is a tendency to spread over the whole area. Whereas this applies intraspecifically to *M. rubra* (and possibly to the other species) it does not apply interspecifically, for both *Formica fusca* and *Lasius acervorum* have a home range, as already pointed out, that is so large as to overlap several such of the Myrmicae.

FORAGING STRATIFICATION

It has already been noted that *Formica fusca* climbed on wire mesh to reach the top of a feeding wick whilst *Myrmica rubra* ascended from below. A further hint of stratification came from the bait studies, for *M. scabrinodis* was rarely seen to take bait sprinkled on the vegetation surface, even when on its nest dome. Such bait was almost invariably collected by *Formica fusca* and *Myrmica rubra*. This could have meant that *scabrinodis* was a nocturnal forager, and yet, in other habitats where compacted areas of bare soil existed (such as heather moor, and paths in fields) its workers could be seen walking over the ground surface by day; and in any case, both the *Myrmicae* are active by night as well as by day.

To test whether species foraging stratification existed or not, traps were set at two different levels: on the soil surface and 7–8 cm above, in the herb layer of ungrazed acidic grassland early in May before the grass had reached its full height. Each trap consisted of a small glass vessel, 2 cm in diameter with sides 2 cm high, half full of a solution of sugar and beer; this was covered with a glass lid that allowed two entrances only, at the rim. Ants find this, drink, fall in, and are asphyxiated. Beer is especially useful as it contains enough alcohol to cause slight narcotization and has a low enough surface tension to cause rapid immersion. By these means, although some workers may escape and set up mobilizations this is reduced to a minimum. The low-level trap was such that the entrance holes were at the soil surface and the high level one was supported from the ground in a stiff wire basket, of 2 cm mesh. Six pairs of traps were set, the units in each pair being 1 m apart and the pairs 10 m apart approximately. The sites were chosen for their high quality as ant areas, not by randomization; all four species were present.

The combined catch produced 666 individuals of five species, the four commonly alluded to, and *M. lobicornis* Nyl. as well. In all, 146 *Formica fusca* were caught, 36 in the higher and 110 in the lower trap; 218 *Myrmica rubra*, 41 in the higher and 177 in the lower; 291 *M. scabrinodis*, 5 in the higher and 286 in the lower. One *Lasius acervorum* and 10 *Myrmica lobicornis* were also collected but in numbers too small for analysis. Thus the three major species all showed a preponderance in the lower traps. Yet *fusca* had 25% in the top, *rubra* 19% and *scabrinodis* only 1·7%. This species deviation from a chance 'average ant' distribution with 12·5% in the top is improbable (χ^2 test: $P < 0{\cdot}001$). *Formica fusca* on the positive and *scabrinodis* on the negative side contributed most of the χ^2 value; *rubra* alone was insignificantly non-average (P: 0·05–0·10). Thus even though it is clear that all species frequent the soil surface it is also clear that the tendency to rise above it, to climb grass stalks, wire mesh, shrubs, etc., is most highly developed in *fusca* and least in *scabrinodis*, *rubra* being intermediate

in this respect. Hence in shortly cropped dense turfy vegetation *scabrinodis* may forage amongst the stem bases, and so escape detection.

Under natural conditions it is also clear when the stratification at a sugar source is recalled and reviewed in relation to these results that the tendency for *fusca* to forage high will be greater in the presence of the Myrmicae than in their absence. It is not that these were dominant over the *fusca*, but simply that they can establish themselves on sugar sources inside the *fusca* home-range, and once established are difficult to dislodge. D. Muir (unpublished) has shown that the Myrmicae forage during a greater variety of weather conditions, and for longer periods in the day and night than *fusca*, which may account for this. Stratification of foraging is common in ant communities; thus in tropical rain forest there are arborial types (*Oecophylla*, *Crematogaster*, etc.), soil surface types (*Pheidole*, *Anomma*, etc.) and hypogaeic types (some species of *Dorylus*). It is also a frequent factor differentiating congeneric species; thus the genera *Lasius* and *Dorylus* both include forms that forage above and others that forage below ground; and Schneirla (1949) has indicated a refined difference (more comparable with the present one), between the species *Eciton hamatum* and *E. burchelli*, the former tending to work lower than the latter.

DISCUSSION

By partial dispersion of feeding areas (intraspecifically) and by partial stratification of feeding zones (interspecifically) the ants in this west Scottish community-type go some way in dense populations to increase the efficiency with which the available food is utilized, even though food supply may not be restricting population growth. Indeed it is doubtful if it ever does except in early seral stages when vegetation (for sugar supply) is sparse; usually it is nesting sites that are scarce, as can readily be shown by providing them artificially when they are rapidly adopted (Brian 1952).

Territory in other ants

So far as is known, all ants maintain a nest territory, but the extent to which areas outside the nest are defended varies considerably. This is no doubt due in part to variation in the evolutionary progress made, but also due to the fact that maximal territorialism (that is the possession of a comprehensive territory) does not necessarily confer the best adaptation; the degree of extranidal control that brings the most benefit for the energy and individual lives expended on its maintenance, depends on the distribution of vital resources. Since ant colonies are relatively sedentary organisms (except Dorylidae) with apterous workers and fairly fixed nest sites they need to obtain as much of their basic requirements as near as possible to the nest in order to avoid unnecessary travel. Soil- or wood-nesting, polyphagy, and the culture of Homoptera have gone a long way towards this, but these requirements are not always compatible with the best micro-climatic conditions, in which case comprehensive territories are extravagant luxuries.

Unlike most animals (except man) the ant attempts to exclude a variety of animals from its domain, not merely other members of its own species, a characteristic perhaps due to its polyphagous habits, for the general resemblance between its foraging and fighting behaviour has already been noted. Its success intranidally has

been so great that many animals—commensals and parasites—have developed special methods of penetration, the study of which has occupied the best-known myrmecologists of the past. The success extranidally varies very much from species to species, and has recently been reviewed by Nixon (1951). Although the most advanced ants have attained to a wide degree of control over tool-animals for obtaining food, and have been able to protect these from climatic and biotic interference, they have not (like man) obtained control over a primary producer—a green plant—although the most advanced harvesting ants come very near to this. Even the fungus cultivators that grow their own food and obtain the benefits of an almost closed nutrient cycle have to collect leaves to replace loss and to increase the turnover.

The following is a brief survey of the varying expression of extranidal territory in ants. The primitive Ponerine ants, *Myrmicia* and *Promyrmecia*, whilst actively defending nest territory (Haskins & Haskins 1950) against their own and other species of ants are simply hunters and collectors of nectar, and in all probability do not defend even small sugar sources for they seem to be totally devoid of recruitment methods. Their foraging system is comparable with that of Vespidae and Bombidae, whose individuals are also able to localize but not recruit more workers to sugar sources.

The evolution of extranidal territory might have occurred with the appearance of primitive pastoralism, for this would not only reduce the area that needed searching, but the fixed groups of Homoptera used could have started as extensions or outposts from the nest territory; many species of Homoptera occur in the nests themselves, feeding on roots and rhizomes. As the organization of the ant evolved, these sources could become larger and farther away from the nest. As an example one can cite *Prenolepis imparis* Say (Talbot 1943) which monopolizes fallen fruit although not at a great distance from the nest, 1·59 yd being the average maximum distance. These territories, although quite definite, lasted only as long as it took to eat the fruit, and the same area might in a single season be the territory of as many as three colonies. These fruits were defended against other insects (flies, wasps, etc.), as well as against the same and other species of ant, but the general terrain, although frequented by scouting workers, was not defended.

A slightly more advanced case involving permanent outposts of Homoptera is represented by such forms as *Lasius niger* which makes covered tracks to groups of aphides on herbs and shrubs. The hypogaeic species *L. flavus* have outposts on plant roots (Carey & Diver 1937). According to Ghilarov (1937) the species *L. niger alienus* gnaws holes in the tap root of *Taraxacum* and inserts aphides. The same species of aphis is put on the lateral roots by the ant *Solenopsis fugax* and, of its own, it feeds on the leaf bases.

Formica rufa may be taken as an example of a further stage in evolution. It may travel over 200 m and monopolize several forest trees which it keeps very clear of other insects. During the summer feeding, at any rate in some habitats, it is almost confined to aphis cultivation, there being very little hunting (Elton 1932). The tracks to these trees from the nests do not cross, although they may pass through branch nests. The community whilst thus split into separate units shows very little evidence of hostility in summer, but in spring it is possible that territories are established with fighting, for Elton saw a large colony destroy a smaller one, taking the ants and brood

back to their own nest and eating them. This type of organized raid, although characteristic of many of the higher Formicidae, appears to be beyond the powers of the member species of the Scottish community. Diver (1935) has mapped a more open community of *F. rufa* with many open spaces and uncolonized trees; he recorded a case of a shared tree but the relations on this were not described. Raignier (1952) has made a special study of a large *F. rufa* community in Belgium. He noted that many species of ant were cleared from this region except *Leptothorax* which survived in tree trunks, and *Stenamma* deep in the soil. The community was divided into sections that were mutually hostile when tested artificially, but natural fighting does not seem to have been very common. Some tracks did not lead to trees, but were highways conducting foragers to hunting grounds into which they filtered over the whole length of the track. Raignier found that a small proportion of workers passed from one section of the community to another like this. Holt (1955) also records far more ground foraging by this species than does Elton; possibly this varies from season to season and place to place. In spring the aphis population is unlikely to be adequate to satisfy the ants, and they may supplement their rations by hunting more. It is not known whether these ground areas are defended or not; this is likely to be much more difficult than the defence of a tree, and in any case the fact that foraging takes place from tracks to owned trees is sufficient to ensure a considerable measure of colony dispersion. The related *Formica sanguinea subintegra* Emery showed a well-dispersed nest distribution in Gibraltar Island, Ohio (Talbot & Kennedy 1940) with permanent trails to nests of the slave species, *F. fusca*, from which they periodically collected pupae. The trails never crossed, although they came near to each other. Food collection which was done by the slaves would presumably follow their characteristic system.

From this stage of territory evolution, two further developments are possible: either the ant nests may be taken into the food area (as in the truly arboricolous ants such as *Oecophylla* and *Azteca*), or food production may take place in the nest (as in the Attini), only raw materials being collected from outside. The arboricolous ants living on and inside myrmecophytes are said to be very aggressive and, at least when their colonies are mature, monopolize whole trees (von Ihering 1891, 1907; Wheeler 1910) feeding from unusually soft tissues of the tree (Bequaert 1922; Bailey 1922). Even so, some animals are not prevented from living on the tree and eating the leaves: the sloth (*Bradypus tridactylus*) and certain caterpillars and Chrysomelid larvae.

Ledoux (1949) and Way (1953, 1954*a*, *b*) have recently produced a lot of information about the feeding system of the tropical ant *Oecophylla longinoda* Latr. which makes leaf-nests in the trees in which it feeds for the most part, and as it defends these trees vigorously and effectively it may be said to have a comprehensive nest-food territory. It feeds partly on insects that alight on the tree, partly on honey-dew from Coccids, and it also eats some of these when they become superabundant in relation to the ant population, throwing others away. Way attaches more importance to the Coccids as a food supply than does Ledoux, a difference of opinion like that over the wood ant *Formica rufa*, which may ultimately be resolved, for hunting may be increased when the Homoptera are too few to supply the protein requirements of the ant. As with the *F. rufa* territories the *Oecophylla longinoda* trees are kept very free of other insects including other species of ant. The arboreal *Crematogaster* and the army-ants (Dory-

lidae) are pillaged as they pass by the tree base, those that venture to leave the trail being snapped up and carried into the nest. But small nests of small species may survive on parts of the tree rarely visited (Way cites species of *Cardiocondyla* and *Tapinoma*). Further *Oecophylla longinoda* appears to be unable to destroy species of *Pheidole* that often nest in the tree base and which destroy small colonies of the dominant ant, particularly where the ground vegetation is so poor that they tend to forage more up into the tree itself.

Oecophylla longinoda no doubt represents the culmination of territorial perfection, and yet it is subordinate to two far less territorial species, *Anoplolepis longipes* and *A. custodiens* (Way 1953). These nest in the ground which has to be almost devoid of vegetation and unshaded; they approach the tree by trackways. In replacing *Oecophylla longinoda* they simply collect the workers as they assemble gesturing aggressively at the base of their tree, and take them back to the nest for consumption. The *O. longinoda* for some reason are in this particular circumstance unable actively to defend themselves as a group. The *Anoplolepis longipes* are far less strict about their territory than the *Oecophylla longinoda*, and tolerate many more species of insect and ant including even large species of *Camponotus*. Way's opinion is that its aggression is purely defensive and directed solely at those that are hostile towards it. In dense populations, *Anoplolepis longipes* showed no division into colonies, and yet (presumably by peaceful means) it was well dispersed over the suitable terrain. Cases like this of dispersion without fighting are not uncommon in other animals (Dice 1952), although it is necessary to show that fighting has never taken place. As long as a species can achieve a desirable degree of dispersion peacefully the way is open to it to form multicolonies, either by accretion with accompanying interchange between initially discrete unit colonies as does *Lasius* spp. (Haskins 1945), or by decentralization through secondary pleometrosis and expansion as in *Iridomyrmex humilis*. It is interesting that the metazoa are thought by Hadzi (quoted in de Beer 1954) to have evolved from protozoa by this latter method rather than by accretion as previously supposed (de Beer 1954). These larger societies, so formed, may show greater assurance, for Forel (1928) and many other authors have noted that this increases with colony size. Perhaps the success of the species *Anoplolepis longipes* compared with *Oecophylla longinoda* in East Africa is concerned with this. But in West Africa *O. longinoda* is itself multicolonial even though fission through isolation in separate trees is common (Ledoux 1949). This species like *Formica rufa* and *Myrmica rubra* may contain subspecies which differ in this precise aspect of social organization.

SUMMARY

1. The feeding system of a four-species community of rather primitive ants characteristic of west Scotland, has been studied. The species were *Formica fusca* L., *Myrmica rubra* L., *M. scabrinodis* Nyl. and *Leptothorax acervorum* Fab.

2. Small sources of sugar could be monopolized, especially if near to the nest, and actual occupation by a group of workers was the main essential to this, although the largest species, *fusca*, could sometimes dislodge the others. The ability to find a source and mobilize feeders on it was a greater guarantee of success than ability in fighting.

3. The hunting distribution of *rubra* was asymmetrical about the nest, even in isolated colonies. In dense groups of colonies, nesting in rotting tree stumps and foraging into long herbs, the same individual asymmetry existed with a tendency for these areas to fit together so that the whole area was searched. These *rubra* home-ranges were entirely overlapped by the much larger ranges of *fusca* and *acervorum*.

4. Three of the species were shown to vary in their propensity to ascend vegetation. *Myrmica scabrinodis* foraged principally on the soil surface and perhaps below, *fusca* readily climbed vegetation, whilst *rubra* was intermediate in this respect.

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THE REPRODUCTIVE CYCLE OF SOME BRITISH FRESHWATER GAMMARIDAE

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(With 7 Figures in the Text)

INTRODUCTION

The general facts of the reproduction of Amphipoda have been described by various workers (e.g. Valle 1887–9; Haempel 1908; Embody 1911; Sexton & Matthews 1913; Sexton 1924; Heinze 1932; Le Roux 1933; Clemens 1950), and the sequence of events is now well understood. Briefly, the adult male takes hold of the female some time before she is ready to oviposit, and the pair remain together in precopula for a few days, until the female moults. Copulation proper then occurs, often several times. The male turns the female round and places his sperm on her ventral surface. The female then breaks away from the male, and before her cuticle hardens the eggs are laid into a brood-pouch made of four pairs of oostegites. The eggs are at first enclosed in a gelatinous sac which slowly dissolves and at about this time fertilization takes place. Hatching occurs after some days and the young leave the mother's pouch after a day or two. She becomes attractive to males again at, or slightly before, the time of hatching of her eggs, and is often to be found in precopula while unhatched eggs remain in her pouch. In most species each female is capable of producing several batches of eggs in succession, and at each moult she grows slightly. The males moult at much longer intervals than the females. The number of eggs laid varies considerably, but on average in any one species larger females lay more eggs (Cheng 1942; Berg 1948; Heinze 1932; Kinne 1952*a*). In some genera it appears that copulation is not preceded by precopula (Watkin 1941). The young mature after a definite number of moults (Sexton 1924; Le Roux 1933; Kinne 1953*a*) which differs in each species. Several instars before maturity it is possible to distinguish the sexes because of the appearance in the male of the genital papillae, which have been figured for *Gammarus pulex* (L.) by Heinze (1932), and in the female of the oostegites, the first appearance of which has been noted in various species by several authors. These appear as small simple plates which enlarge at each moult, and which acquire serrated edges at the last moult before maturity, at which stage the developing eggs in the ovaries are clearly visible. At maturity the oostegites become fringed by long bristles, which interlace with one another and form the brood pouch, figured by Heinze (1932). No breeding females are ever without these bristles. Legueux (1924) and Heinze (1932) noted, in *Gammarus duebeni* Lillj. and *G. roeselii* (Gervais) respectively, that breeding females can lose these bristles at a subsequent moult and return to the condition of serrated edges, although the oostegites remain larger than those of immature specimens. Le Roux (1933) further found that this effect could be produced by sterilization with radium, and was connected with ovarian activity. Kinne (1953*b*) has made a detailed

study of this phenomenon in *G. duebeni* and found that it occurs seasonally and is probably connected with temperature fluctuations. It may intervene before maturity or after one or more batches of eggs have been laid. He and Le Roux have both shown that after a few instars these females re-acquire the bristles and breed again normally.

Many authors (e.g. Embody 1911; Le Roux 1933; Sexton & Matthews 1913; Sexton 1924; Mottram 1934) have investigated the length of the various stages of several species of Gammaridae under various laboratory conditions, and Kinne (1952*a*, *b*, 1953*a*–*c*), in a series of admirable papers, has studied *G. duebeni* so thoroughly that he has been able to match his laboratory findings in great detail with the behaviour of the species in the field (Kinne 1953*d*).

Some workers have made detailed studies of the life-cycle in the field. Blegvad (1922) investigated *G. locusta* (L.), but unfortunately his results are dubious because his population was later shown to consist of several species (Segerstråle 1947). Some species of other families have been studied in this way, e.g. *Corophium volutator* (Pallas) by Watkin (1941), and *Pontoporeia affinis* Lindstrøm by Mathisen (1953). Within the family Gammaridae Kinne has, as already stated, achieved a clear understanding of the life-cycle of *G. duebeni* in brackish water, and I (Hynes 1954*a*) have been able to confirm some of his work and extend it to include the rather different cycle in fresh water. A few other freshwater Gammaridae have been studied in the field; i.e. *G. fasciatus* Say (Clemens 1950), *G. lacustris* Sars (Dahl 1915; Berg 1938) (both these authors refer to this species as *G. pulex*, but Stephensen (1940) and Kaiser (1941) have corrected their determinations), *G. pulex* (L.) (Berg 1948) and *Pallasea quadrispinosa* Sars (Mathisen 1953). The present investigation was undertaken with the object of bringing our knowledge of the life-cycle in Britain of *G. lacustris* and *G. pulex* into line with that of *G. duebeni*, and of finding out something about the life histories of *G. fasciatus* (= *G. tigrinus* Sexton, Hynes 1954*b*) and *Crangonyx gracilis* Smith. The last two species are of North American origin, which have somehow been introduced into Britain (Hynes 1955). Little is known of their life-cycles here (Sexton & Cooper 1939), although Embody (1911) made some observations on them in North America, and Clemens (1950) has made a detailed study of *Gammarus fasciatus* in Lake Erie.

METHODS

Periodic samples of each species were collected from a single locality throughout a year, and as far as was feasible these were taken at monthly intervals. Longer intervals were necessary for *G. lacustris* because of the distance from Liverpool of the only suitable locality. The shrimps were collected with a fine stramin hand-net, and an effort was made to make the samples as random as possible. For *G. pulex* the net was worked in the cloud of debris made by kicking up the stream bed with the feet as described by Hynes (1954*a*). For the other species the net was worked amongst vegetation and debris and under stones. The contents of the net were transferred at intervals to a dish, and this was repeated until it was judged that sufficient specimens had been obtained. The samples of *G. pulex* were preserved in the field in formalin and later sorted by the flotation method used earlier for *G. duebeni* (Hynes 1954*a*). Unfortunately

this method could not be used for the other three species as the samples were full of light vegetable matter and they had to be hand-sorted on return to the laboratory while the animals were still alive. This was not only tedious, but for the samples of *Crangonyx gracilis*, and possibly also those of *Gammarus fasciatus*, in which several litres of material had to be sorted, it seems certain that it resulted in the loss of some of the smallest specimens, despite the care taken. When the collections were made the water temperature was measured and an estimate made of the number of pairs in precopula.

The shrimps were fixed in 5% formalin, in which they were also examined, and were later stored in 90% alcohol containing 2% glycerin. In each sample every specimen was measured, from the front of the head to the base of the telson, while straightened out over a scale, to the nearest millimetre, or for *Crangonyx gracilis* half-millimetre, below. This method of measurement tends probably to underestimate the length of the individual, but as all were treated in the same manner the various samples were strictly comparable. In practice each shrimp was not actually measured, but was matched against a series of specimens 1·5, 2·5, etc., mm long. In this way it was possible comparatively rapidly to place most individuals shorter than 12 or 13 mm long in their size-group. Larger specimens, and those about which there was doubt, were measured individually.

Each specimen of *Gammarus* longer than 6 mm. below which length it was difficult to separate the sexes, was then examined and placed in one of the following classes: male, ovigerous female, female with young in brood pouch, female with fully bristled oostegites but empty brood pouch, female with fully developed but bristleless oostegites (occasionally a few scattered bristles are found on these specimens), immature female. Each male *G. fasciatus* was examined for the presence or absence of curly hairs on the antennae and legs; these have been considered to be diagnostic of the species (Sexton & Cooper 1939) but are not present at all seasons. Similarly, about 50 males of *G. pulex* more than 9 mm long were examined from each sample for the presence or absence of curly hairs on the third leg, which also are normally considered diagnostic (Schellenberg 1942) but which are not always present. A few males of both these species were found to have small oostegites. In other respects these specimens were normal males. All specimens of *Crangonyx gracilis* were examined, and each was placed in one of the following classes: mature male, immature male, ovigerous female, female with young, female with fully developed and bristled oostegites but empty pouch, immature female, unsexable juvenile. No females with fully developed but bristleless oostegites were found. The maturity of the males was determined by the presence or absence of the large elongated calceoli on the flagellum of the antennae which are very conspicuous in adult males of this species.

The number of eggs of each ovigerous female was recorded, as was the number of young in the pouch of each female with young, and the state of development of the eggs was also noted. Three states were arbitrarily recognized as follows: early, with little or no cleavage; developing, with a comma-shaped embryo with more or less developed appendages; late, embryo fully developed with eyes. For *Gammarus pulex* and *G. lacustris* the last two stages were not distinguished as the samples were not

examined immediately after collection, and it was not always possible to be sure about the later stages of development. In all four species newly laid eggs were found to be enclosed in two mucous sacs as described in *G. fasciatus* by Clemens (1950).

In addition to the regular samples which were analysed as outlined above, two similar series of samples of *G. pulex* were collected from other localities and were examined in less detail. Also a number of samples of this species and of *G. fasciatus* were collected from other places at suitable seasons in order to determine if the same general cycle of events occurred everywhere.

Some laboratory investigations were made on such things as length of time needed for hatching of eggs, time taken to reach maturity, number of egg-batches laid per female, etc. Most of this work was done with *G. fasciatus* and *Crangonyx gracilis*, and stocks of both these species were kept under close observation in large aquaria. The more detailed observations were made on specimens kept in shallow water in glass-covered flat enamelled dishes, which were maintained at room temperature and examined about once every 10 days. The shrimps were fed on elm leaves and *Cladophora* and chopped *Tenebrio* larvae. These observations were made only to augment and clarify those made on the field samples, and no attempt was made to go into details, such as number of moults to maturity which have been closely studied in some species by other workers (e.g. Sexton 1924, Le Roux 1933, Kinne 1953*a*, Clemens 1950).

GAMMARUS PULEX PULEX (L.)

Regular samples were collected from three localities:

(1) Shotwick, Cheshire; altitude 15 m; a small sluggish silty stream with a gravel bed, 2–3 m wide and 10–20 cm deep, heavily shaded by trees, without rooted vegetation but with much vegetable debris. *G. pulex* was abundant, and associated fauna included oligochaetes, *Asellus aquaticus* (L.), *Baetis rhodani* (Pictet), *Nemoura cinerea* Retzius, *Sialis lutaria* (L.), *Plectrocnemia* sp., *Agapetus fuscipes* Curtis, *Limnophilus* sp., *Simulium* sp., large numbers of Chironomidae, *Limnaea pereger* (Müller) and *Gasterosteus aculeatus* L. In December 1949 the water contained chloride 40 mg/l, calcium 31 mg/l, and magnesium 11·5 mg/l.

(2) Richmondhill, Isle of Man; altitude 50 m; a medium swift stony stream 2 m wide and 20 cm deep, flowing beneath trees beside damp pasture; moss and *Lemanea* present on the larger stones. *Gammarus pulex* was common but not abundant, and the associated fauna was similar in type to that found in the R. Terrig (below). In April 1950 the water contained chloride 26 mg/l, calcium 14 mg/l and a trace of magnesium.

(3) R. Terrig, Rhydtalog, boundary between Flintshire and Denbighshire; altitude 300 m; a small swift stony stream 1–2 m wide and up to 30 cm deep, flowing through open moorland and upland pasture, with dense patches of *Callitriche*. *Gammarus pulex* was abundant, and associated fauna included *Polycelis cornuta* (Johnson), oligochaetes, *Baetis rhodani*, *Rhithrogena semicolorata* (Curtis), *Ecdyonurus torrentis* Kimmins, *Isoperla grammatica* (Poda), *Chloroperla torrentium* (Pictet), *Capnia bifrons* Newman, *Leuctra hippopus* Kempny, *L. fusca* L., *Brachyptera risi* (Morton), *Amphinemura sulcicollis* Stephens, *Nemoura cambrica* Stephens, *Rhyacophila* sp., *Plectrocnemia* sp., *Agapetus fuscipes*, *Stenophylax* sp., *Halesus* sp., *Helodes* sp., *Helmis maugei*

Bedel, *Simulium* sp., Orthocladiinae, *Dicranota*? sp., *Ancylastrum fluviatile* (Müller) and *Salmo trutta* L. In December 1949 the water contained chloride 11 mg/l, calcium 14 mg/l and a slight trace of magnesium. In addition, samples were collected in mid-winter from streams in Anglesey and Surrey and Hertfordshire.

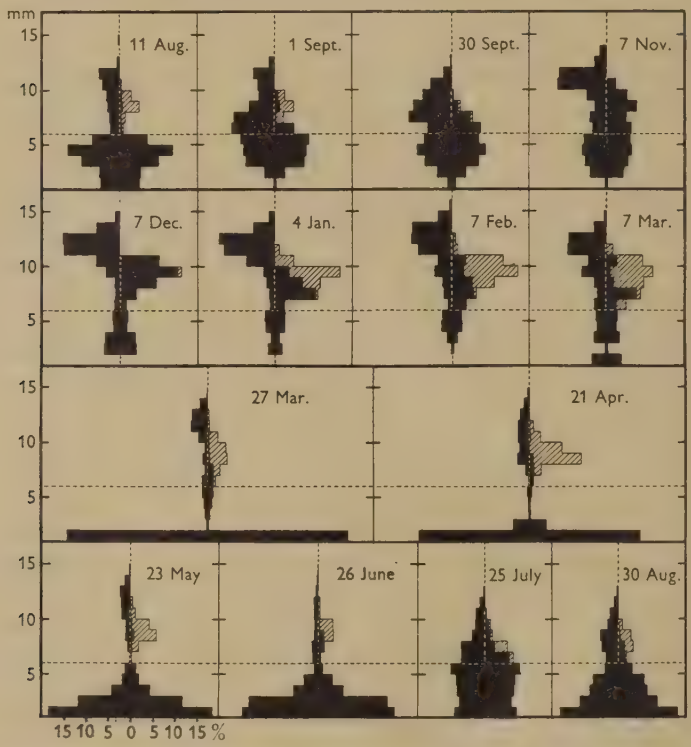

Fig. 1. Size and sex distribution in samples of *Gammarus pulex* from Shotwick, 1949–50. The length of the shrimps is given by the vertical scale, and the length of each horizontal size-group block represents the percentage of the total in that size-group. The horizontal dotted line (at 6 mm length) shows the lower limit of sex distinction: below this line the blocks are centred; above it males are shown on the left and females on the right. Females shown by the cross-hatched areas had fully bristled oostegites.

Fig. 1 shows details of the samples from Shotwick, and further information is given in Table 1. These show that breeding, i.e. the presence of very small specimens and females with fully bristled oostegites, slowed down during September, and that none occurred during November. In December a few females began to produce eggs, and the number of these increased rapidly, reaching a peak in April and May, and then slowly declined. The first young appeared in the sample taken in early March, and large numbers appeared between then and June. The largest of the new generation became mature in July and August.

If one assumes, as seems reasonable, that this cycle of events is repeated year after

Table 1. Gammarus pulex, *Shotwick, Cheshire, 1949 and 1950. Details of the regular samples*

Averages are bracketed when based on fewer than ten specimens.

Date of sampling	11 Aug.	1 Sept.	30 Sept.	7 Nov.	7 Dec.	4 Jan.	7 Feb.	7 Mar.	27 Mar.	21 Apr.	23 May	26 June	25 July	30 Aug.
No. of specimens	473	346	603	509	405*	447*	384*	480	1337	960	1574	1326	1470	1597
Specimens < 6 mm long as % of total	71·1	48·8	48·7	38·8	20·4	13·9	12·0	23·7	69·0	58·8	75·7	85·2	66·7	75·0
Ovigerous females†	14·6	6·8	1·3	0	1·6	20·8	27·8	23·0	24·6	39·6	39·7	26·6	14·0	12·6
Females with young†	0·7	0	0	0	0	0	0	4·0	2·4	1·3	3·7	1·5	1·2	2·5
Mature females with empty brood pouches†	9·5	5·5	0·6	0	0	2·6	3·8	5·6	8·7	14·2	8·4	9·7	2·5	5·8
Females with large but bristleless oostegites†	2·9	2·8	1·3	5·5	23·0	7·5	1·8	0·8	0·7	0·3	2·1	0·5	1·6	0·5
Females/males (all specimens longer than 6 mm)	0·49	0·34	0·37	0·58	0·82	0·95	1·15	1·06	1·00	1·65	1·29	1·26	0·72	0·54
Mature females‡/males > 8 mm	0·53	0·41	0·07	0·10	0·48	0·64	0·77	0·78	0·84	1·58	1·34	1·27	0·76	0·55
% of males > 9 mm long without curly hairs§	4·0	11·8	44·5	46·0	0	0	0	0	0	0	0	2·0	2·0	2·0
No. seen in precopula (estimated)	Many	Some	None	None	Some	Few	Some	Many	Many	Many	Many	Few	Few	Few
Water temperature, ° C	15·0	14·8	13·5	6·5	6·8	8·2	3·5	5·7	6·2	9·8	11·5	15·3	15·0	14·5
Average no. of eggs per ovigerous female	11·9	12·9	(13·0)	—	(25·6)	22·0	16·7	16·8	17·3	15·6	17·4	13·6	9·6	9·8
Average length of ovigerous females	8·4	8·2	(8·0)	—	(9·5)	9·6	9·7	9·4	8·9	9·0	9·0	9·1	7·8	8·4

* No specimens < 2 mm long.
† As percentage of specimens > 6 mm long.
‡ Including those with large bristleless oostegites.
§ Based on the examination of about 50 specimens.

year, it is possible from the data to get some indication of the length of life of individuals in the field. Specimens born in March become mature in July and breed through August and early September. They then cease breeding, begin again in January, and continue to breed during the spring. It is not possible to determine when they die, but it is probably in April or May. Specimens born later in the summer, say June and July, overwinter as juveniles and do not mature until March; they then breed through April, May and June. Between the June and July samples there is a sharp fall in the mean size of the adults of both sexes, and this probably represents the death of most of the remaining overwintered animals; one can fix the death of these as late June. Therefore under summer conditions (temperature 10–15° C) the shrimps take 3–4 months to mature, and under winter conditions (5–10° C) about 7 months.

One can also get information from the sex ratio. Considering all animals longer than 6 mm (Table 1) one finds that in autumn there were about three times as many males as females. This is because the males being larger were the first of the new generation to reach this size. There is also the possibility that, in this species as in *G. duebeni* (Kinne 1952*b*, 1953*c*), temperature is sex determining and that the males are born earlier in the season than the females. During the early winter the proportion of females increased; by December and January most animals were longer than 6 mm and at this time the sex ratio was about 1:1. This is the true sex ratio of the species. During the spring the proportion of females rose still further to about 5:4. This may be due either to a true slight preponderance of females or to the earlier death of some of the males. The fact that there was at the same time a drop in the proportion of larger males indicates the latter. The fall in the proportion of females in the later summer was due to the growth to more than 6 mm of some males of the new generation. It seems therefore that in contrast with *G. duebeni* (Hynes 1954*a*) the males of this species may have a slightly shorter life than the females, although, of course, there remains the possibility that they are actually born earlier in the season.

I have made few laboratory observations on *G. pulex*, but have found that specimens take about four months to reach maturity at room temperatures (15–20° C); Mottram (1934) gives this figure as about 100 days. Sexton (1924) gives figures of numbers and lengths of instars from which it is possible to calculate that the ten moults before maturity need about 70 days in summer and 180 in winter. Haempel (1908) states that only 90 days are needed for maturity at 8° C, but it is not clear whether he is referring to *G. pulex* or to *G. roeselii*.

The number of batches of eggs laid by each female of this species is stated by Heinze to be six to nine. The lower number would appear to be that reached in the field. In the Shotwick samples the first post-resting period eggs were found in early December, but no young appeared until early March. At winter temperatures therefore incubation takes about three months. Sexton (1924) states that in summer, at temperatures which were probably higher than those in Shotwick stream, incubation takes 16–17 days; assuming that a new oviposition occurs almost at once this represents about three weeks per batch. So, interpolating, a female who starts breeding in December will produce broods in about early March, mid-April, early May, late

May, mid-June and possibly early July when she dies, and she may have already produced one brood in the previous autumn.

The short resting period in early winter is of considerable interest. In its general features it resembles that found to occur in autumn in *G. duebeni* (Kinne 1952*a*, Hynes 1954*a*). The number of breeding females decreased during the autumn until, by the end of September, females with fully bristled oostegites composed only about 2% of the specimens longer than 6 mm (Table 1). At the same time the number of females with large unbristled oostegites increased, but did not reach its maximum until December. It is clear, therefore, that many of the females in the resting stage in November, December and January had not already bred, but had entered this state of suspended maturity directly from their immaturity. From this it follows either that there was a heavy mortality among the specimens, born in early spring, which began to breed in late summer, or that in fact very few actually attained maturity before the onset of colder weather. Fig. 1 shows that some specimens did mature in the summer of their birth; these first appeared as mature in the July sample. The mean size of these females increased until early September, and after that there was a sharp drop in mean size. This seems to indicate that there was in fact heavy mortality of these females during September.

The males of this species also show morphological evidence of the resting stage. Adult males longer than about 9 mm normally have curly hairs on the third pereopod, and these are used as a specific character (Schellenberg 1942); in very large males they are occasionally present on the fourth pereopod also. During the resting period many of the males were found to be without these curls (Table 1); although the hairs were present they were straight. I have no direct evidence that individual males of this species actually lose their curls, but as this definitely does occur in *G. fasciatus* there is reason to suppose that they do. It would seem therefore that any male who moults at this season loses his curls, and possibly also that as with the females, young males reaching mature size during this period, do not acquire this secondary sexual character. Laboratory tests showed that males without curly hairs would not enter into precopula. No specimens were found in precopula during the resting period (Table 1), but as no females were ready to mate it cannot be stated certainly whether the males that had retained their curls would in fact have taken females. It seems likely, however, that all the males were sexually inactive and only those which actually moulted at this season showed this morphologically. This would explain why the percentage of males without curls did not rise to 100. It is known that male *Gammarus* moult far less frequently than females (Kinne 1953*a*, Sexton 1924, 1928). A further point of interest is that the males began to re-acquire their curls before the females re-acquired their bristles. This can be seen in Table 1, and more clearly in Tables 2 and 3. The males therefore recover from the resting period before the females, which thus have no shortage of mates as soon as they are ready for them.

The samples from the River Terrig and Richmondhill were studied in less detail than those from Shotwick; results are shown in Tables 2 and 3. From these, and Fig. 2, where some of the data are plotted for comparison, it can be seen that the general cycle of events was the same in all three localities. In the Isle of Man, however, a few ovigerous females were found during the resting period, the production of

Table 2. Gammarus pulex, *Richmondhill stream, Isle of Man, 1949 and 1950. Details of the regular samples*

Date of sampling	29 Aug.	23 Sept.	22 Oct.	23 Nov.	30 Dec.	27 Jan.	24 Feb.	18 Mar.	13 Apr.	12 May	14 June	12 July	11 Aug.
No. of specimens	712	1358	1170*	393	273*	323*	464	256	372	231	563	480	1129
Specimens < 6 mm long as % of total	67·2	84·6	71·1	30·1	38·1	31·6	47·9	48·0	53·8	46·9	62·2	57·3	76·0
Ovigerous females†	27·9	24·4	5·3	3·3	4·7	13·1	18·2	19·1	15·7	16·8	21·1	17·1	24·2
Females with young†	0·9	0·9	0·3	0	0	0	0·8	0·8	0	2·4	0·9	2·4	1·5
Mature females with empty brood pouches†	9·0	6·7	0·3	0	0	0·9	0·8	1·5	2·3	2·4	0·5	1·0	0·7
Females with large but bristleless oostegites†	0	0·9	4·7	10·5	4·7	1·4	2·1	0	0	0·8	0	0	0
Mature females‡/males > 8 mm	1·06	0·93	0·31	0·38	0·29	0·40	0·80	0·34	0·74	0·82	0·62	0·69	0·97
% of males > 9 mm long without curly hairs§	0	14·0	54·0	36·0	32·5	10·0	6·0	0	0	0	0	4·0	3·9
No. seen in precopula (estimated)	Many	Many	Few	Few	Some	Many	Many	Many	Many	Many	Few	Few	Few
Water temperature, ° C	14·8	14·2	10·1	9·7	7·7	6·0	6·9	9·3	10·1	12·5	14·8	16·4	15·2

* No specimens < 2 mm long.
† As percentage of specimens > 6 mm long.
‡ Including those with large but bristleless oostegites.
§ Based on the examination of about fifty specimens.

Table 3. Gammarus pulex, *R. Terrig, Rhydtalog, Flintshire/Denbighshire, 1949 and 1950. Details of the regular samples*

Date of sampling	1 Sept.	30 Sept.	7 Nov.	8 Dec.	9 Jan.	7 Feb.	7 Mar.	27 Mar.	21 Apr.	23 May	26 June	25 July	30 Aug.
No. of specimens	722	996	849*	288	664*	811*	1115	1006	991	2414	2751	2520	1979
Specimens < 6 mm long as % of total	52·5	62·6	47·9	32·6	41·3	22·9	47·6	59·5	51·2	77·0	83·2	82·1	77·8
Ovigerous females†	11·9	2·7	0·2	0	10·0	21·1	11·5	30·8	30·6	26·2	25·7	21·9	12·5
Females with young†	0·9	0	0	0	0	0	0·2	2·7	1·2	3·0	1·5	1·1	0·9
Mature females with empty brood pouches†	2·9	1·6	0·2	0	0	0·8	0·9	2·0	1·0	2·0	4·6	5·5	2·7
Females with large but bristleless oostegites†	0·6	2·7	14·4	15·4	4·1	6·7	2·2	0·7	1·0	0·4	0·4	1·5	1·4
Mature females‡/males > 8 mm	0·50	0·30	0·47	0·46	0·79	0·64	0·84	0·84	0·99	0·97	0·75	0·61	0·42
% of males > 9 mm long without curly hairs§	3·8	42·0	24·0	22·0	16·2	2·0	0	0	0	0	0	0	0
No. seen in precopula (estimated)	Many	None	None	Few	Few	Some	Some	Many	Many	Many	Few	Few	Few
Water temperature, ° C	14·0	11·4	6·5	5·1	7·9	2·5	6·5	8·5	8·5	12·5	14·9	14·0	15·9

* No specimens < 2 mm long.
† As percentage of specimens > 6 mm long.
‡ Including those with large bristleless oostegites.
§ Based on the examination of about fifty specimens.

young occurred fairly steadily throughout the summer, and there was not the same peak in breeding activity in spring. Because all the specimens longer than 6 mm were not sexed it is not possible to discuss the sex ratio in the way that was done for Shotwick. The ratio of adult females (including those with large bristleless oostegites): males longer than 8 mm, which should give some idea of the sex-ratio of breeding specimens, although probably a little weighted in favour of the males, has, however, been worked

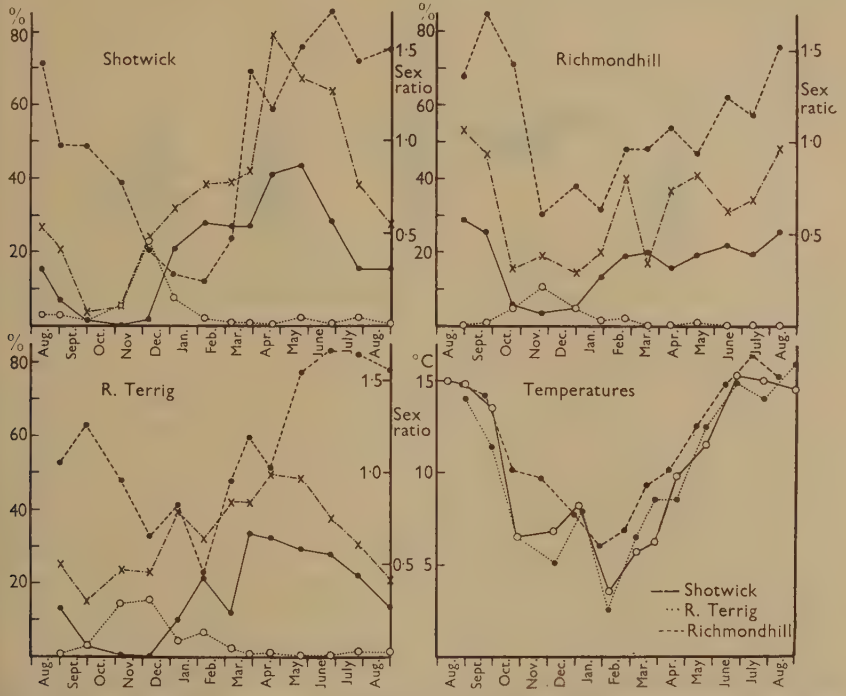

Fig. 2. Seasonal trends in composition of populations of *Gammarus pulex* in three localities, and water temperatures. *Trends*: -●--●-, specimens less than 6 mm long as % of total; —●—●— breeding females, ··○···○··, females in resting stage, both as % of specimens longer than 6 mm; -·-×-·-×-·-, sex ratio (mature females/males longer than 8 mm).

out for all three stations (Fig. 2 and Tables 1–3). This followed the same general trend in all three localities, but it is of interest to note that in late spring and early summer this figure did not rise above 1·0 at Rhydtalog and Richmondhill. This militates against the suggestion, made above, that the males die off before the females, or shows that it may only apply to particular conditions.

Two of the midwinter samples from the Isle of Man have been plotted in detail in Fig. 3, as have the samples from Hertfordshire, Surrey and Anglesey, of which details are given in Table 4. The Manx, Hertfordshire and Anglesey samples closely resemble those from Shotwick except that not all the Manx females had entered the resting period, and that the Hertfordshire sample more nearly resembled the September sample from Shotwick than the November sample. The latter may well be merely a

reflexion of the particularly mild autumn of 1953. The Surrey sample was, however, rather different in that no small specimens were present. This was certainly not due to bad collecting, and the sample differed also in that the number of females with large bristleless oostegites was particularly high. It would seem that this may be the result of higher summer and autumn temperatures prevailing in a sluggish southern stream, which enabled all the young to reach adult or near adult size before the resting period set in. It may be noted here that the Surrey stream was much smaller and more sluggish than the Hertfordshire stream.

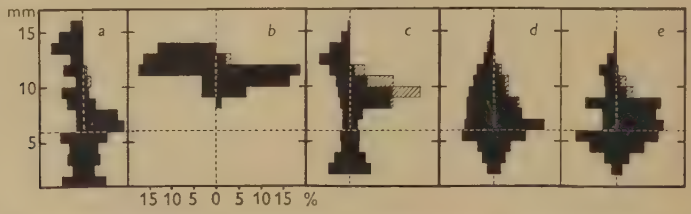

Fig. 3. Size and sex distribution in winter samples of *Gammarus pulex*. Arranged as in Fig. 1. *a*, Kimpton, Hertfordshire, 13 Nov. 1953; *b*, Ockham, Surrey, 6 Dec. 1952; *c*, Pen Lloegr, Anglesey, 6 Jan. 1950; *d* and *e*, Richmondhill, I.O.M., 23 Nov. and 30 Dec. 1949.

Kinne (1953*b*) has suggested that a fall from high summer temperatures accounts for the resting period of *G. duebeni* in late autumn, and has evidence that it can be produced at other seasons in the laboratory by sudden lowering of the temperature. In that species the oostegites remain without bristles usually for two instars, and then breeding recommences in early winter. In *G. pulex* the same explanation seems reasonable, although here the steep temperature drop is later in the year (September–October, Fig. 2) because of the relatively low summer temperatures of the habitat. This results in a resting period during November and December, and sexual activity starts again in late December and January, even though temperatures may still be falling slowly. In this connexion it is significant that the resting period was less marked in the Manx station than in the English and Welsh ones, and that this is correlated with a less steep autumnal drop in temperature and higher winter temperatures (Fig. 2). Presumably either not all females were affected, or they were not affected simultaneously because of less definite stimulus, and the high winter temperatures allowed the bristleless instars to be passed quickly so that a few were found to be ovigerous both in November and December. Similarly, it would seem that the mild autumn of 1953 caused the onset of the resting period to be rather later in Hertfordshire in that year than at Shotwick in 1949.

It is obvious that if this explanation is correct the time of the resting period and its length will vary with different years and different climates. This would account for the fact that Kaiser (1941) reports finding breeding specimens in all months among many collections from Denmark, whereas Berg (1948), working in the same area but in one year and place, reports that reproduction seems to cease in winter, although breeding specimens were found in early spring in very cold water (1–2° C). Dr T. T. Macan has also informed me that in a small stream, Smooth Beck in the

Lake District, in which he collected weekly samples during 1949 and 1950, he found no pairs in precopula during October, November and early December, very few ovigerous females in November, and none in December and the first week in January. His results, and those of Berg, therefore confirm the general existence of a winter resting period over a wide area.

Table 4. Gammarus pulex. *Details of some winter samples*

Items marked with an asterisk are expressed as % of specimens >6 mm long. Items marked by a dash were not estimated.

	Kimpton, Hertfordshire	Ockham, Surrey	Pen Lloegr, Anglesey
Date of sampling	13 Nov. 1953	6 Dec. 1952	6 Jan. 1950
No. of specimens	242	91	407
Specimens <6 mm long as % of total	39·8	0	25·9
Ovigerous females*	1·4	0	20·2
Females with young*	0·7	0	0·3
Mature females with empty brood pouches*	0·7	1·1	1·3
Females with large but bristleless oostegites*	2·8	38·4	14·9
Females/males (all specimens >6 mm)	0·65	0·84	1·46
% of males >9 mm long without curly hairs	41·7	—	—

The life-history of *G. pulex* would appear therefore to be as follows. Some adults and many immature specimens overwinter. During January to March they begin to breed and continue to do so until midsummer or a little later, each female laying five or six clutches of eggs. This generation then dies, and there are perhaps indications that the males may die first, which is a contrast with *G. duebeni* in which the males outlive the females (Hynes 1954*a*). The sex ratio is about 1:1; again this is in contrast with *G. duebeni* where females greatly outnumber males (Kinne 1952*a*, Hynes 1954*a*). The new generation grow during the summer and a few of them reach maturity in July and August. The temperature then falls steeply in the autumn and breeding ceases in early winter. Apparently there may be considerable mortality among the mature individuals at about this time. No breeding occurs during the early winter and at this time adult females lose their oostegite bristles and the males may lose their curly hairs; similarly, juveniles reaching adult size at or just before this season do not acquire these characters. Breeding recommences in January, and the breeding population is steadily increased until April or May by the maturing of young specimens born late in the previous summer. Temperature therefore controls the cessation of breeding but not its onset, although presumably with very low temperatures the resting season would be longer because of increased intervals between moults. Growth of individuals continues during the winter at quite low temperatures, and if the winter temperatures are high and the autumn temperature fall slight, a few specimens may be found breeding even in November and December.

As shown in Table 1, the average number of eggs per female in the samples from Shotwick was highest at the beginning of the breeding season, and lowest in late summer. This fluctuation was due to the varying mean size of the females, which itself resulted from the life-cycle outlined above. As is well known, larger females carry on average more eggs than smaller ones, and this has been shown in *G. pulex*

by Heinze (1932) and Berg (1948). This was also found to apply at Shotwick as follows:

Length of female (mm)	6–7	7–8	8–9	9–10	10–11	11–12
No. of specimens	20	117	300	297	123	17
Mean no. of eggs	5·8	8·9	13·4	18·0	23·6	29·1

The mean number of eggs of all females examined was 16·0, but the range of variation was great (1–43). The fluctuation of mean number of eggs per female throughout the year was therefore due to the proportions of the various females of the two generations in the samples. In January the first females to start breeding were those that had already bred, and so were large. Young specimens then matured during the next four months and so lowered the average and kept it down. Then during June the older females began to die off, and in July and August small females of the new generation began to breed and the last of the older females disappeared. The average number of eggs and of mean size of female was then at a minimum and rose slowly through the autumn as the young females grew.

Kinne (1952*a*) found in *G. duebeni* that in all size-groups the average number of eggs per female was highest at the height of the breeding season in spring. There was no evidence of this in the Shotwick samples where the mean number of eggs per female of any given size-group varied little but quite erratically month by month. Similarly, Kinne (1952*a*) found that in *G. duebeni* the mortality rate of the eggs in the brood-pouch was lowest in the spring. In *G. pulex* there appears to be no such mortality in the brood-pouch. The mean number of eggs in the early stages of development was 15·7 (406 females, all months) and in the later stages 16·2 (468 females). The mean number of young was only 9·1 (62 females) but this was more probably due to some young specimens having already left their mothers than to mortality.

GAMMARUS LACUSTRIS Sars

Eight periodic samples were collected from Llyn Llywenan, Anglesey, altitude 30 m, during the year May 1953 to April 1954. This lake is large (about $1 \times 0{\cdot}5$ km) but shallow (maximum depth 2 m), and for much of its length the shore is reed-swamp, where aquatic birds abound. At one point the shore is fine gravel. Where the samples were collected the substratum was silty sand with a dense sward of *Littorella* with patches of *Elodea* and *Ranunculus*. Large loose stones occured at intervals and *Gammarus lacustris* was at all times abundant under these. The fauna was rich and varied and included *Polycelis* sp., *Stylaria lacustris* (L.) and other oligochaetes, *Glossiphonia* sp., *Erpobdella* sp., *Piscicola geometra* (L.), *Daphnia* sp., *Asellus meridianus* Rac., Hydracarina, *Argyroneta*, *Coenis* sp., *Ishnura elegans* (V. d. Lind), *Plea leachi* McGreg. & Kirk., *Corixa* spp., *Phyrganea* sp., *Traienodes* sp., Leptoceridae, Polycentropidae, *Limnius tuberculatus* Müller, *Deronectes depressus* Fabr., *Haliplus* sp., *Sphaerium corneum* L., *Physa fontinalis* (L.), *Planorbis* spp., *Limnaea* spp., *Gasterosteus aculeatus* L., *Pygosteus pungitius* (L.), *Anguilla vulgaris* L., and *Salmo trutta* L. The conductivity of the water varied from 150 to 206 μmho, and the water contained chloride 46·5 mg l, calcium 15 mg l, magnesium 10 mg l, sodium 22 mg l, and potassium 1·7 mg l. This particular locality was chosen for study as it is the only

known lake within reach of Liverpool where *Gammarus lacustris* is both common and not mixed with *G. pulex*. Very small specimens of these species cannot be separated. The outflow of the lake was without a population of *Gammarus*, although a few stray specimens of *G. lacustris* were found near the lake.

The samples were analysed in the same manner as were those of *G. pulex*, except that specimens infected with acanthocephalan larvae were treated separately from uninfected specimens. A large proportion of the population was at times found to be infected (Table 5), the larvae being clearly visible as red bodies beneath the cuticle of the shrimps. It was apparent that infection delayed the growth of the hosts. This is discussed fully below. Fig. 4 and Table 5 give details of the samples. Considering only the uninfected specimens, which are shown on the left in each frame in the figure, it can be seen that in May large numbers of young were present. These grew steadily during the summer, autumn and winter and began to breed between late November and early February, and the first young of the new generation were hatched during April. The old generation persisted until July, but were by then much reduced in numbers, and very few were still present by the end of August. Very few newly hatched young were present in early July and none were found later than this. It is clear therefore that the species has a strictly annual cycle. Specimens born in April and May become mature in February and March, breed through May and die during June and early July.

The change in the sex ratio (Table 5) shows that the males die before the females. In August the ratio was about 0·8 females per male, indicating a ratio of about 1:1. If, as seems probable, all the unsexable juveniles in the sample were females this ratio was actually 1·07:1. During October and November the ratio was of the same order, but then the proportion of females rose steadily until by April it was 2·20:1. In the May sample it was 2·74:1 and in July was 12·00:1 if one considers only the old generation; the figure 0·75 given in the table includes also some young males of the new generation. The breeding period is short in this species, and it is clear from Fig. 4 that the first batch of eggs took two months or more to incubate. Later batches undoubtedly took much less time, because at room temperatures (*c.* 18° C) incubation took about three weeks. The temperature became higher than this in the lake after May, so it seems probable that each female was able to produce three and some even four clutches before her death in June or July.

In *G. pulex* there is in each year a period during which mature females cease to breed and lose their oostegites. No such phenomenon was found in *G. lacustris*, as the females die after breeding. In this respect *G. lacustris* resembles *Pontoporeia affinis* Lindstrøm and *Pallasea quadrispinosa* Sars (Mathisen 1953). Only one female was found, in July, with fully developed but bristleless oostegites. She may have bred previously, but it is equally possible that for some reason she did not mature. In February about half the non-breeding females had large but bristleless oostegites, but these were obviously immature specimens which would mature at the next moult. It may be noted, however, that the oostegites of many of these females were as large as those of mature specimens. There may therefore be a resting period before maturity, as there is in many specimens of *G. pulex*.

In the laboratory various collections of shrimps were kept under close observation

Table 5. Gammarus lacustris, *Llyn Llywenan, Anglesey, 1953–54. Details of the samples*

Figures are bracketed when based on fewer than ten specimens.

Date of sampling	22 May	10 July	31 Aug.	13 Sept.	27 Nov.	10 Feb.	15 Mar.	27 Apr.
Total no. of specimens	1042	730	300	491	148	438	296	453
Specimens < 6 mm long*	85·3	95·9	10·3	0·3	0	0	(0·4)	51·4
Ovigerous females†	34·9	(25·0)	(0·6)	0	(0·7)	16·6	58·1	31·4
Females with young†	11·6	0	0	0	0	0	0	6·5
Mature females with empty brood pouches†‡	23·3	(14·3)	(0·6)	(0·3)	0	(1·4)	(1·8)	28·5
Females/males (all uninfected specimens > 6 mm)	2·74	0·75	0·78	0·71	0·79	1·35	1·52	2·20
No. seen in precopula (estimated)	Many	None	None	None	None	Half	Few	Many
Water temperature (° C)	15·5	19·2	14·5	11·9	10·0	2·0	5·0	11·2
Average no. of eggs per ovigerous female	21·4	(13·5)	(11·0)	—	(19·0)	19·5	23·2	22·8
Average length of ovigerous female	11·8	(11·6)	(12·5)	—	(12·5)	11·1	11·4	11·4
Infected specimens as % of total	4·7	6·4	31·0	23·8	9·5	2·5	5·1	2·9
Infected specimens as % of generation born 1952	25·1	42·9	(0)	(0)	—	—	—	—
Infected specimens as % of generation born 1953	—	3·7	31·2	23·9	9·5	2·5	5·1	5·5

* Uninfected specimens as % of all specimens not infected with *Polymorphus minutus*.
† Uninfected specimens as % of uninfected specimens > 6 mm long.
‡ Including the one female found in July which had bristleless oostegites.

in dishes. Specimens hatched in late May grew at about the same rate as those in the field and began to oviposit in early February. They thus followed the cycle in the field very closely, although the temperature of the laboratory was higher. Three females kept at a mean temperature of about 18° C required 20, 21 and 22 days for incubation of their eggs.

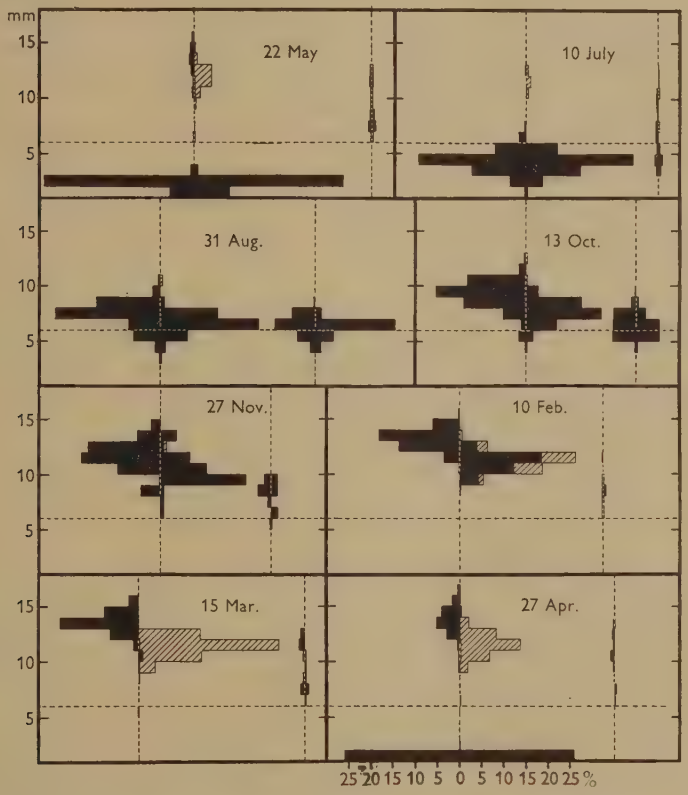

Fig. 4. Size and sex distribution in samples of *Gammarus lacustris* from Llyn Llywenan. Arranged as in Fig. 1, except that specimens infected with *Polymorphus minutus* are shown separately to the right of each sample, and percentages are those of uninfected specimens instead of total.

Six pairs of adults collected in the field were isolated on 11 February, at a time when the females were either immature or newly ovigerous with their first batch of eggs. They were kept under observation until the females died, and any males which died were replaced. These females produced, 4, 4, 5, 5, 5 and 6 batches of eggs before their death, and the four that produced more than four batches survived until the end of July, the end of August, and early September, and one was still alive on 20 September, although she had laid no eggs since early June. They therefore lived considerably longer than most of their generation in the field. The two females who produced four batches died in early July and mid-August, and it would seem that

four batches of eggs probably represents the maximum number produced in the field. The females kept in the laboratory were, throughout the spring when the water of the lake was cold, kept at about 18° C. They were therefore able to incubate their eggs more rapidly. So, as already stated, three, or at most four, batches of eggs are probably produced in the field. The long survival of the specimens kept in the laboratory was probably due to good feeding and protection from enemies. The same phenomenon was noted in *G. duebeni* (Hynes 1954*a*). Nearly all the clutches of eggs laid hatched normally and large numbers of young were produced. On a few occasions no young could be found, but this was probably due to cannibalism, as, apparently, all the eggs were retained for their full term in the brood pouches.

In the field the mean number of eggs per female increased with the size of the female as follows:

Length of female (mm)	9–10	10–11	11–12	12–13	13–14
Number of specimens	18	83	148	83	9
Mean number of eggs	15·7	19·0	22·4	24·2	28·2

The mean number of eggs of all the females examined was 21·8, and the range of variation large (1–40). There was no evidence of mortality of the eggs in the brood-pouch. The mean number of eggs in early stages of development was 21·4 (202 females) and in the later stages 22·2 (139 females). As in *G. pulex*, the mean number of young in the brood-pouch was much lower (9·9; 30 females). As shown in Table 5, the mean number of eggs per female rose a little during the early breeding season (February to April), and this can be correlated with a slight increase in size of female. It then fell rapidly, and in July the few ovigerous females were carrying very few eggs.

Two workers have previously studied the life-cycle of this species. Dahl (1915) made his investigations in Norway, and Berg (1938) in Denmark. In both places the general cycle of events appears to be the same as was found in Anglesey, although in Norway the main breeding season is later in the year. Dahl found ovigerous females abundantly in June and a few in July and August. Berg concludes that the cycle is strictly annual, but Dahl suggests that growth to maturity at least for some specimens takes nearly two years. This was because he found some immature specimens during June. Re-examination of his data in the light of my findings and those of Berg indicates, however, that this conclusion is probably invalid. Almost all his immature specimens were 7 mm or more long in June when breeding commenced and this is only 1 mm shorter than the few small specimens in the corresponding March sample from Llyn Llywenan. He records also a few smaller specimens in June, but these were an insignificant proportion of his sample and may well have been specimens stunted by infection with Acanthocephala (see below). It would also appear from his tables that Dahl's sampling technique did not catch many of the very small specimens, and that this fact rendered his results less easy to interpret than mine. It is clear, however, from his tables that the main season of production of young in Norway is July and August as opposed to April and May in Anglesey and May and June in Denmark.

The size of individuals of both sexes appears from Dahl's paper to be greater in

Norway than in Denmark and Anglesey. Berg states that males in Denmark are 15 mm long or less, and in Llyn Llywenan the largest males were just over 16 mm, and the largest females just over 14 mm long. In northern Norway Dahl found one male 22 mm long and many of 20 or more, and females up to 17 and 18 mm or more. In southern Norway most males were shorter than 18 mm and only one of 19 mm was recorded and most females were 16 mm long or less and only one of 17 mm was found. It is possible therefore that length varies inversely with latitude or temperature.

Specimens infected with Acanthocephala

Dr Prudhoe identified the larvae in some of my *G. lacustris* as *Polymorphus minutus* (Goeze), a common parasite of ducks. Most of the infested specimens contained one larva, but multiple infections were common, particularly in the August and October samples when the rate of infection was high (Table 5 and Fig. 4), and as many as seven larvae were observed in one shrimp. Le Roux (1933) has shown that this species causes castration of the female of *Gammarus pulex* and a slowing down of the development of secondary sexual characters in the male, who is, however, not castrated.

All the infected specimens in the samples were measured and examined for sex condition. It was found that they tended to be considerably smaller than uninfected specimens of the same generation. This is shown by the May, October, November, February and March samples (Fig. 4). It was also found that nearly all the infected females were immature and had small bristleless oostegites. Of the total number of 54 infected females in the May, July, March and April samples, in which a very large proportion of the uninfected females were breeding, only five showed signs of maturity. Of these one had six eggs, all of which were dead, and four others had small oostegites on which there were a few bristles. There were also two specimens with large bristleless oostegites. It is obvious, therefore, that infection interferes very seriously with breeding, and probably prevents it altogether. In the laboratory infected specimens lived well and survived for many months, but neither there nor in the field were specimens of either sex observed in precopula. There was also no evidence that a shrimp once infected ever lost the larva.

There are no data to show how long the larva of *Polymorphus minutus* takes to reach full size and become clearly visible in the shrimp, but indirect evidence indicates that this may take three weeks or more. On two occasions young specimens were brought into the laboratory and apparently uninfected individuals were selected and kept in dishes, and in both samples a few infected specimens were observed after three to four weeks. As, however, the water in which they were kept came from the lake it is possible that *P. minutus* eggs were introduced into the dishes.

Fig. 4 and Table 5 show that the percentage of infection varied throughout the year. In May 1953 about one in four of the old generation were infected, and this figure was nearly one in two in July. This may indicate that the non-breeding infected individuals survive a little longer in the early summer than the normal ones, or it may represent fresh infection. By July some of the new generation had become infected and by the end of August over 30 % of the population were infected. The proportion fell steadily

until September, but during the winter and spring it became stabilized at about $2\frac{1}{2}$–5%. From this it would appear that the main period of infection was July and early August, that small infected specimens tended to die off fairly rapidly, but that those that survived, possibly because they were larger and so better able to withstand the parasite, overwintered. In 1953 it appeared that overwintering infected specimens survived rather longer than non-infected specimens.

The suggestion that the summer is the main period of infection with *P. minutus* and that infected specimens die off during the autumn is supported by some scattered observations made on a population of *Gammarus duebeni* in a stream at Ballabeg, Isle of Man. Once again I am indebted to Dr Prudhoe for the identification of the parasite. The source of the infection is unknown, but it may have been domestic geese. In late July 1949 over 25% of the 205 *G. duebeni* collected were infected, but in September only about 10% were infected. In April 1950 fewer, possibly 5%, were still infected. During that summer no observations were made and no infected specimens were seen in January 1951, although several hundreds were examined. In November 1951, however, between 5 and 10% were infected, and by April 1952 this had fallen to about 2%. At the end of July 1953 a further large sample was collected, and although no counts were made, my notes state that *Polymorphus minutus* was common. It would seem therefore that the parasite was only found to be abundant in samples taken in the summer, that it was less common in the autumn and relatively rare or even absent in the winter and spring. Although these observations are incomplete and were made only incidentally during other work on *Gammarus duebeni*, they agree well with the more detailed results obtained for the parasite in *G. lacustris*.

Reid (1951) has remarked on the sudden, unaccountable disappearance and subsequent re-appearance of large populations of *G. lacustris* in west Sutherland, and noted that Loch Poll a Chnoic lost a population of many years' standing between April and August 1947. Such violent fluctuations in number have not been reported in other freshwater amphipods. It seems possible that *Polymorphus minutus* could cause such fluctuations. The arrival in a lake of a large flock of heavily infected ducks would result in the death or castration of a large proportion of the *Gammarus*, and this might well result in almost complete elimination of *G. lacustris* from a lake in a short while. *Polymorphus minutus* occurs in other freshwater species, e.g. *Gammarus duebeni* (above) and *G. pulex* (Le Roux 1933) but these species, unlike *G. lacustris*, are not confined to lakes. Ducks, quite apart from the fact that they tend to occur in large flocks more on lakes than on streams, would be unlikely to infect the whole length of a river. Even though they might almost eliminate populations from lakes there would, in these other species, always remain large reserve populations in inflowing streams. *G. pulex* has been shown to spread both up and down a stream into which it had been introduced (Hynes 1954*a*), so movement into a depleted lake would probably occur fairly rapidly. This suggested ability of *G. pulex* to withstand infection may be one of the reasons why it would appear that this species is replacing *G. lacustris* in British lakes (Hynes 1955).

GAMMARUS FASCIATUS Say (=*G. TIGRINUS* Sexton, Hynes 1954*b*)

Regular samples were collected from drainage dykes on Frodsham Marsh, Cheshire, during the year October 1952 to September 1953, and two further samples were collected in January and June 1954. These dykes lie below high tide level and drain clayey agricultural land. They flow towards the River Weaver, but connexion with the river, which is tidal but controlled by locks, is through a pumping station. This operates only at certain river levels, so flow in the dykes is intermittent and the water is almost static for long periods each day. The collections were made in the main dyke, which is about 4 m wide and 1·5 m deep at its highest level, and in the lower 100 m of a smaller side dyke, where collecting was easier at times of high water.

The two dykes were similar, with substrata of black mud overlying clay. There were dense beds of *Myriophyllum spicatum* L., *Potamogeton crispus* L. and *P. pectinatus* L. and some *Lemna minor* L., *Elodea*, *Callitriche* and *Enteromorpha intestinalis*. The fauna was rich and varied, the following animals being common: Tubificidae, *Glossiphonia* sp., *Ishnura elegans* (V. d. Lind), *Halipus* sp., *Hydroporus* sp., *Noterus capricornis* Herbst., *Corixa striata* L., Chironomidae, *Potamopyrgus jenkinsi* (Smith), *Limnaea pereger* Müller, *Physa fontinalis* (L.), *Gasterosteus aculeatus*, and *Pygosteus pungitius*. Several other species of molluscs and insects including *Sialis lutaria* (L.), were present in small numbers and a few specimens of *Palaemonetes varians* (Leach), which is common in other parts of the dyke system, were seen. *Gammarus* was frequent, but nowhere abundant, although the shrimps tended to congregate in patches of decaying plants. They were thus found chiefly in *Myriophyllum* in the winter and early spring, and in *Potamogeton crispus* in late summer. Most were *Gammarus fasciatus*, but about 5 % were *G. duebeni*. The two species occurred together in the same loci. Further upstream in the side dyke, above the sampling point, a few specimens of *G. pulex* were found. These were in a region of swifter flow, where the water was fresh.

The water in the dykes at the point of sampling was distinctly saline, presumably because of seepage of sea water from the Manchester Ship Canal and the River Weaver, both of which skirt the marsh and lie at a higher level. The conductivity varied from 648 to 1795 μmho, being highest in periods of summer drought and generally lower in winter, although in June 1953 after heavy rain it fell to its lowest level. On 16 January 1953, when the conductivity was 847 μmho, the chloride content was 287 mg/l, calcium 126 mg/l, and magnesium 55 mg/l. On 18 February 1953 when the conductivity was 1221 μmho, calcium was 115 mg/l, sodium 152 mg/l, and potassium 11·1 mg/l. It seems, therefore, that the water in the dyke was a varied mixture of sea water and hard fresh water.

The samples, which contained much weed, were sorted by hand, and it was early apparent that relatively few of the smallest specimens were found. This was not entirely due to their being missed in the samples, and it was at first thought that the young might inhabit different loci from the adults, as was found of '*G. locusta*' by Blegvad (1922) and of *Corophium volutator* (Pallas) by Watkin (1941). Investigation in an aquarium showed that, as reported by Clemens (1950), the young of this species tend to occur on the bottom. So, however, do the adults, and care was always taken

to stir up the bottom when samples were taken. In Wyken Slough, near Coventry, where two collections were also made, large and small specimens were obtained together in great numbers. It seems probable, therefore, that the relatively small number of young specimens in the Frodsham samples, and hence possibly also the fact that the species was far less abundant there than at Wyken Slough, was due to heavy predation. It was found in the laboratory that *Gasterosteus aculeatus* and nymphs of *Ishnura elegans*, both of which were abundant in the dykes, would eat incredible numbers of very small *Gammarus fasciatus*, whereas they did not harm larger specimens.

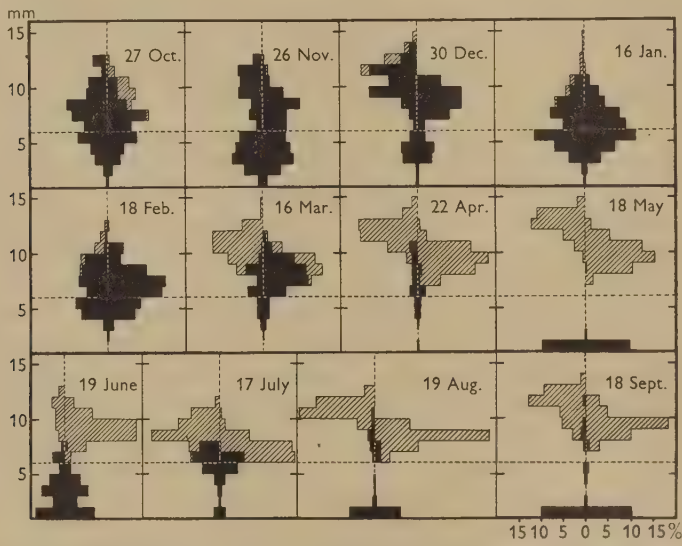

Fig. 5. Size and sex distribution in samples of *Gammarus fasciatus* from Frodsham. Arranged as in Fig. 1, except that males with curly hairs are shown by cross-hatched areas.

Fig. 5 and Table 6 show details of the samples. From these it can be seen that no breeding occurred during the winter (November to February), but that it began in early March and continued during the summer. All the females were immature or in the resting stage with bristleless oostegites during the winter months, and none of the males in the October sample had curly hairs, although there were some breeding females. The larger males began to acquire curly hairs in December, and nearly all had done so by mid-March, at which time some of the females were ready to breed. It was not possible to assess the degree of curliness in the males, but those found in midwinter were definitely less curly than those found in the spring and summer. No males without curly hairs were ever found in, or induced to engage in, precopula. The first young appeared in early May; by mid-June a few of these had become mature, and many more were mature by mid-July. The old generation began to disappear during late May, as is shown by the decrease in mean size of adults between the May and June samples; probably most of the old generation had gone by mid-July,

Table 6. Gammarus fasciatus, *Frodsham Marsh, Cheshire, 1952–54. Details of the regular samples*

There are intervals of several months between the last three samples. Averages are bracketed when based on fewer than ten specimens.

Date of sampling	27 Oct.	26 Nov.	30 Dec.	16 Jan.	18 Feb.	16 Mar.	22 Apr.	18 May	19 June	17 July	19 Aug.	18 Sept.	15 Jan.	3 June
No. of specimens	185	235	111	474	345	514	233	238	143	448	205	169	414	76
Specimens < 6 mm long as % of total	29·7	47·3	18·9	45·2	30·1	7·2	3·9	20·1	39·1	14·7	13·6	22·5	14·2	0
Ovigerous females*	12·3	0	0	0	0	11·5	25·0	29·5	34·5	23·1	36·7	37·4	0·3	39·5
Females with young*	1·5	0	0	0	0	0	1·3	10·0	9·2	5·8	5·1	7·6	0	0
Mature females with empty brood pouches*	2·3	0·8	0	0	0	0·6	24·1	18·9	33·4	12·8	9·0	12·2	0	1·32
Females with large but bristleless oostegites*	3·1	4·8	2·2	0·4	2·1	4·0	0	0	0	0	0	0	17·2	0
Females/males (all specimens > 6 mm)	0·93	1·10	0·73	0·90	1·38	0·99	1·15	1·44	3·58	0·96	1·18	1·01	1·38	1·11
% of males without curly hairs (all specimens > 6 mm)	100·0	100·0	97·5	89·8	83·2	21·0	14·5	0	26·3	24·5	9·8	7·6	50·4	0
No. seen in precopula (estimated)	None	None	None	None	Few	Many	Many	Many	Some	Some	Some	Some	None	Some
Water temperature, ° C	7·8	0·5	2·0	6·0	6·7	6·8	16·9	17·7	18·8	16·4	15·8	13·9	9·8	14·0
Average no. of eggs per ovigerous female†	34·0	—	—	—	—	25·4	28·0	44·4	21·7	14·7	27·0	44·2	(26·0)	?
Average length of ovigerous females	9·9	—	—	—	—	8·6	9·3	10·0	9·2	7·5	8·4	9·2	(11·0)	10·3

* As percentage of specimens > 6 mm long.

† Based on from 16 to 90 specimens except for Jan. 1954 which is represented by one specimen only.

as there was a further drop in mean size of adults between the June and July samples. The new generation continued breeding through August and September.

Unfortunately illness prevented my taking samples in October, November and December 1953, but samples were collected in January and again in mid-June 1954 (Fig. 6, Table 6). From these it is clear that as in 1952–53, breeding ceased during the winter and began again in early summer. There were, however, two marked differences between the samples taken in the different years. Although there is some irregularity between the various winter samples of 1952–53 (Fig. 5) it is clear that the overwintering specimens were smaller than those of 1953–54. In fact, the largest specimens of both sexes were collected in January 1954 (Fig. 6). Similarly, the percentage of females with large but bristleless oostegites was much larger in January 1954 than in 1953. This is

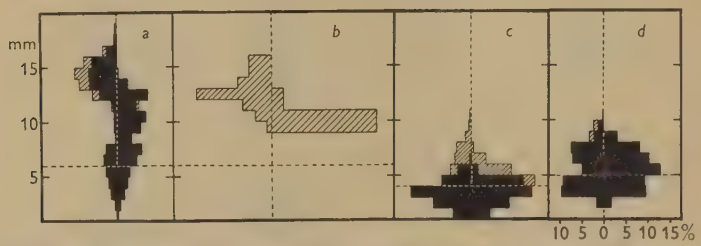

Fig. 6. Size and sex distribution in samples of *Gammarus fasciatus*. Arranged as in Fig. 5. *a* and *b*, Frodsham, 15 Jan. 1954 and 3 June 1954; *c* and *d*, Wyken Slough, Warwickshire, 26 Aug. 1953 and 17 Feb. 1954. In the last two samples the lower limit of sex-distinction is 4 and 5 mm respectively.

almost certainly a reflexion of the very mild autumn of 1953, which allowed many more of the new generation to mature, and to continue growing after the onset of the resting period. Similarly, the cold spring of 1954 probably accounts for the difference between the June samples. Table 6 shows that by early June 1954 the water temperature had risen only to 14·0° C, whereas in April 1953 it was already higher than this. The onset of breeding was presumably greatly delayed and no young had been produced by early June 1954. The temperature between January and June had, however, been high enough to enable even the smallest specimens to become mature. It may be noted here that none of the ovigerous females had hatched their eggs by early June, whereas females with young were found during the last half of April 1953 (Table 6).

The sequence of the two generations is also shown by the mean numbers of eggs per female (Table 6). These show two peaks in May and September, representing periods when the females were large. The persistence of some females of the 1952 generation until mid-June 1953 is shown by the fact that the mean number of eggs was higher in the June than in the July sample.

As in the other species there was a clear correlation between length of female and mean number of eggs. This was also shown by Clemens (1950).

Length of female (mm)	6–7	7–8	8–9	9–10	10–11	11–12	12–13
No. of specimens	37	74	117	106	66	23	5
Mean no. of eggs	10·8	15·5	22·8	32·5	49·3	52·4	78·4

The mean number for all females was 29·3, and the actual number very variable (1–86). As in the other species there was, within any one size-group, no consistent seasonal variation in mean number of eggs.

The sex-ratio in most samples was about 1:1 (Table 6). The only exception to this was the sample taken in June 1953, where females greatly outnumbered males. This may have been due to a sampling error; the sample was small and was taken at a time of particularly high water which made collecting difficult. Or it may indicate that, as in *G. lacustris*, the males of the old generation tend to die before the females.

In order to determine whether the annual cycle was similar elsewhere samples were collected in August 1953 and February 1954 from Wyken Slough, near Coventry, Warwickshire, the locality where the species was first discovered in Britain. This is a suburban boating lake covering several hectares. On the west shore, where the collections were made, the bottom was mud partly overlain by large stones, and there were a few small clumps of *Typha*. During the summer there were dense growths of *Potamogeton pectinatus* L. and some *Myriophyllum spicatum* L., *P. crispus* L. and *Chara*, and all these plants were encrusted with chalk. During the winter only a few plants of *Myriophyllum spicatum* and *Potamogeton obtusifolius* Mert. & Koch. were seen. The water was muddy and somewhat polluted with oil and was bright green with phytoplankton in the summer. Many fishermen angle here for roach, rudd and perch, and specimens of *Cottus gobio* and *Gasterosteus aculeatus* were seen. *Gammarus fasciatus* was enormously abundant; there must have been many thousands to the square metre. Other animals were relatively scarce; amongst them Tubificidae, *Asellus*, Zygoptera, *Chironomus*, *Potamopyrgus jenkinsi*, *Limnaea pereger* and *L. stagnalis* (L.) were observed. A sample collected for me in April 1951 by Dr R. W. Butcher, presumably from another part of the lake, contained several other species of mollusc, *Corixa striata* (L.), *Limnophilus* sp. and *Crangonyx gracilis* Smith.

The water of this lake is known to be saline (Sexton & Cooper 1939). In April 1951 Dr Butcher recorded pH 7·9, chloride 533 mg/l and temporary hardness 290 mg/l calcium equivalent. In February 1954 the conductivity was 1580 μmho, chloride 290 mg/l, sulphate *c.* 200 mg/l, calcium 166 mg/l, magnesium 49 mg/l and sodium 282 mg/l. The lake is thus, like the dykes at Frodsham, an unusual habitat. In England this species seems to be confined to such localities (Hynes 1955), although in Ireland, and in North America, it occurs in quite fresh water.

Details of the two samples are shown in Fig. 6 and Table 7. It is apparent that the species was much smaller than at Frodsham, and because of this it was possible in the August sample to determine the sex of all specimens longer than 4 mm; indeed some females in the 4–5 mm group were mature. In the February sample, however, only about half the specimens in this group could be sexed with certainty. This indicates, as already found in Lake Erie by Clemens (1950), that specimens mature at a smaller size in summer than in early spring. This can also be seen to have applied at Frodsham if, for instance, the April and July samples are compared (Fig. 5). The August sample from Wyken Slough did not resemble that from Frodsham, although it was similar in that active breeding was occurring, but the February sample, apart from the disparity in adult size, was similar to the samples collected at Frodsham during the winter of 1952–53. It would seem, therefore, that although the general cycle of events

was the same at the two places there were differences in timing. Possibly the warm spring of 1953 did not so rapidly raise the water temperature at Wyken Slough, with the result that the new generation began to appear later, as appears to be likely to have occurred also at Frodsham in 1954. This would result in a higher proportion of small overwintering specimens, which was in fact found.

Table 7. Gammarus fasciatus, *Wyken Slough, Warwickshire. Details of the samples*

Items marked with an asterisk are expressed as % of sexable specimens, i.e. longer than 4 mm in August and 5 mm in February.

Date of sampling	26 Aug. 1953	17 Feb. 1954
No. of specimens	2561	924
Unsexable specimens as % of total	52·7	40·6
Ovigerous females*	25·2	0
Females with young*	1·7	0
Mature females with empty brood pouches*	2·7	0
Females with large but bristleless oostegites*	0	3·3
Females/males, all sexable specimens	1·38	1·35
% of males without curly hairs	50·4	92·7
No. seen in precopula (estimated)	Many	None
Water temperature (° C)	17·0	4·6

In the laboratory it was found difficult to rear the species in small dishes, possibly because they were not properly fed (Clemens 1950). The incubation period for two females was found to be 16 days at a mean temperature of 16° C, and at about this temperature the young took 13 weeks to mature. At a mean temperature of 23° C they took only six weeks and specimens kept at 2° C were not mature after eight months, although they had grown to lengths of 6–9 mm. The only female who lived and bred successfully under close observation produced and hatched six batches of eggs during her three and a half months of adult life. These results are in general agreement with those of Clemens. These observations show therefore that, although the species can live and grow at quite low temperatures, the time taken to reach maturity is greatly influenced by temperature. Clemens found that the same applies to incubation periods and time between moults. Observations made in dishes showed also that in late autumn individual breeding specimens collected in the field and brought into the laboratory ceased to breed, as they did in the field. At the next moult the females lost their oostegite bristles and the males their curly hairs. This occurred even though they were no longer subjected to falling temperatures.

That the resting period is not controlled by low temperatures as such was perhaps shown by observations on a population in a large tank. This was stocked with mud, weed and water from Frodsham, and placed in a warm place in the laboratory. Fifty breeding pairs of *Gammarus fasciatus* were introduced in May 1952 and the sequence of generations was watched. By mid-June large numbers of young were present, and the old specimens had all died by mid-July. The new generation grew rapidly and began to breed in early July. Many of these adults disappeared during September and October and only a few and their offspring remained. The latter grew during the late autumn and early winter and many reached adult size during December. Despite the fact that the temperature was still fairly high (*c.* 14° C) no breeding occurred, and

although the temperature rose steadily to *c.* 17° C at the end of March, no breeding activity occurred until the end of April. This was actually over a month later than the onset of breeding in the field the year before, despite the much higher temperatures. There is, however, reason to believe that the resting period observed in this tank was due to shortage of suitable food. This is discussed more fully below.

The life-cycle of this species in Britain would appear to be as follows. A generation is born in early summer, and in a cold season such as that of 1954 this may be delayed until midsummer. These specimens mature rapidly and begin to breed in the autumn. At the end of September breeding ceases and those specimens already mature enter a resting stage. During the winter and very early spring the young born in the autumn mature and most are ready to breed when sexual activity recommences in March and April. Under exceptional conditions, e.g. in the tank, a second generation may be produced during the summer. In late autumn breeding ceases, and the size and maturity composition of the population which overwinters depends on the climate of the previous summer. If breeding began late, as apparently it did in Wyken Slough in 1953, or a second summer generation has been produced, as in the tank, many of the overwintering specimens will be juveniles. If, however, breeding was early, many of the overwintering specimens will be adults, as at Frodsham in 1953–54. If this occurs there would seem to be a tendency for very large specimens to be produced.

These suggestions are in general agreement with the findings of Clemens in Lake Erie, but there are a few points of difference due to the much lower summer temperatures of the British localities. For instance, in Britain the difference in mean size of mature females was not found to fall so sharply from spring to summer as in Lake Erie, where temperatures of 24–25° C were recorded in July and August, and in the autumn there was a distinct rise in size of mature females at Frodsham, due to the ageing of the females and the lack of recruitment from their offspring. Presumably this was due to the lower temperatures, which did not enable specimens born in July and August to become mature. It would seem therefore that this species is at a disadvantage in the low and unstable temperatures of the British summer. It is capable of very rapid breeding and growth at quite high temperatures, but below about 15° C quite small changes in temperature cause big alterations in the durations of its various stages. In this connexion it is of interest to note that I have the impression that in Frodsham in 1953 the first batch of eggs laid by the females produced no young. Many specimens were ovigerous in mid-March, but despite the fact that by 22 April the temperature had risen to 16·9° C, at which temperature incubation takes only about 16 days, very few young longer than 2 mm were found in the May sample. As the species grows rapidly at the then prevailing temperatures this must mean that almost all the young, which one would expect to have been born in April, had either been destroyed or that something had gone wrong with the eggs laid, and for some time carried, at temperatures below 7° C. It has already been suggested that predation was heavy at Frodsham, and this may be the explanation, but observations made at the time point to a failure of the brood. Twenty ovigerous females brought into the laboratory on 16 March all shed their eggs within 3–7 days of capture, and ten females captured in precopula laid eggs in the laboratory, but these also all failed to hatch. Shedding of the eggs is a common reaction in all species when for some reason they

fail to develop, so it would seem that the whole of the first brood was unsatisfactory. It would seem therefore that this species is adapted to a climate in which the summers are warm, and the springs accompanied by a rapid rise in temperature, but that it is able to withstand and to grow at temperatures as low as 2° C. (This sentence was written before it was realized that *G. tigrinus* was in fact *G. fasciatus* (Hynes 1954*b*), and it describes almost exactly the sort of climate in which Clemens investigated the species in its natural habitat in North America.) Possibly it is because the species is not truly suited to our climate that it seems unable to compete with *G. pulex* (Hynes 1955). It seems likely that it would prove more successful in southern Europe, or in small ponds which become very warm in the summer.

CRANGONYX GRACILIS Smith

Monthly samples were collected from the R. Dee, Llangollen, Denbighshire, altitude about 90 m, from October 1952 to September 1953. The river here is wide and swift, flowing over slabs of bare rock covered with moss, and through deep pools. Salmon and trout are common. The locus from which all the samples were collected was a strip of *Glyceria maxima* (Hartm.) along the right bank of the river. This grass, and others, were emergent at the water's edge and the shrimps occurred amongst the grass and in the vegetable debris beneath it. They were never found far from the bank, except at times of low water, and then only in vegetable debris. The fauna here included oligochaetes, several species of mayflies (*Centroptilum*, *Leptophlebia*, *Paraleptophlebia*) and of stoneflies (*Leuctra* spp., *Taeniopteryx*), *Corixa scotti* D. & S., *Micronecta poweri* (D. & S.), *Haliplus* sp. and *Phoxinus* as well as *Gammarus pulex*, which was far less common than *Crangonyx gracilis*. The conductivity of the water varied from 55 to 87 μmho, being lowest at times of flood, and the calcium content (three samples) from 10·7 to 12·5 mg/l. *C. gracilis* was found in similar sheltered habitats for several miles downstream from the sampling point.

Details of the samples are shown in Table 8. It is probable that many of the smallest juvenile specimens were not collected, as the sorting had to be done by hand, and the smallest specimens were sluggish and difficult to detect. They were, however, present in all samples. From the table it is clear that there was no annual cycle, such as was found in *Gammarus*. There was, in fact, no marked difference in the composition of the population month by month, and the differences which do exist between the columns of the table were almost certainly due to sampling errors. The monthly samples have not therefore been drawn out in detail as for the other species, but the composition of all the samples together is shown in Fig. 7. This gives some idea of the general structure of the population, sizes of the two sexes, etc., although the very small specimens were undoubtedly under-represented in the samples. Study of the individual samples showed only a few points of difference which may perhaps be seasonal. The largest immature females were collected in December, January and February, and the largest immature males were found in February and March. Similarly, the largest mature females were collected in February and March and the smallest in May, June and August. Perhaps, therefore, cold retards maturity a little and warmth accelerates its onset. Similarly, and probably for the same reason, the

Table 8. Crangonyx gracilis, *River Dee, Llangollen, Denbighshire. Details of the regular samples, 1952 and 1953*

Items marked with an asterisk are expressed as % of total number of specimens. Averages are bracketed when based on fewer than ten specimens.

Date of sampling	21 Oct.	26 Nov.	30 Dec.	29 Jan.	27 Feb.	24 Mar.	30 Apr.	29 May	26 June	22 July	31 Aug.	30 Sept.
No. of specimens	131	264	242	282	174	295	197	440	510	480	274	572
Juveniles*	16·8	23·8	21·1	12·8	19·0	10·2	18·8	32·5	32·2	20·6	24·8	39·4
Ovigerous females*	4·6	7·6	5·8	3·2	4·0	7·1	13·7	4·5	4·1	8·1	6·6	5·2
Females with young*	0	1·1	1·2	0·4	0·6	0·7	1·5	1·4	0	0·2	1·1	0·5
Mature females with empty brood pouches*	4·6	4·9	5·4	1·4	0·6	2·3	3·6	3·9	4·9	4·4	4·0	4·0
Immature females*	33·6	24·6	31·4	39·4	26·4	31·1	21·8	20·5	16·7	24·6	24·1	17·1
Mature males*	29·8	12·1	19·0	20·2	35·1	26·4	36·0	32·5	30·6	35·6	31·4	24·6
Immature males*	10·7	25·7	16·1	22·7	14·4	22·4	4·6	4·8	11·5	6·5	8·0	9·1
Females/males (all sexable specimens)	1·06	1·01	1·25	1·03	0·64	0·84	1·00	0·86	0·61	0·89	0·91	0·78
Females/males (mature specimens only)	0·31	1·12	0·65	0·25	0·15	0·37	0·52	0·30	0·29	0·36	0·37	0·40
Water temperature (° C)	7·8	2·1	3·2	2·4	5·6	8·0	8·3	14·3	19·4	15·8	14·8	13·7
Average no. of eggs per ovigerous female	(24·7)	33·6	26·8	(31·3)	(50·8)	54·7	42·8	34·0	31·2	26·9	27·8	29·2
Average length of mature female (mm)	7·3	7·3	7·3	7·3	(8·0)	7·8	7·4	7·0	7·1	7·0	6·7	7·0

average size of the mature females collected in February, March and April, and with this the mean number of eggs, was larger than at other seasons. Otherwise there appeared to be no seasonal variation whatever; the average size of the mature males, for instance, varied quite irregularly. There was no indication of a resting stage, and even though some of the largest females had bristleless oostegites (Fig. 7) these specimens were clearly immature as their oostegites were small.

The sex ratio seemed to be about 1:1 at all times. For all specimens it was 1 male:0·863 female; that more males than females were actually found was probably because the sex of the males could be determined at a smaller size than that of the

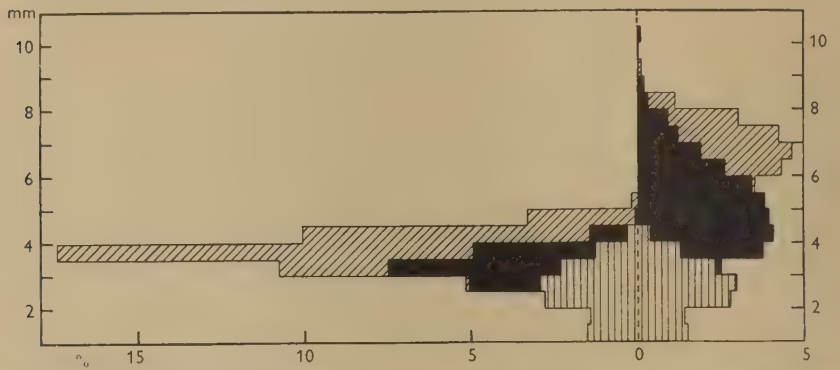

Fig. 7. Size and sex distribution in all samples of *Crangonyx gracilis* from R. Dee, Llangollen, 1952–53. Arranged as Fig. 1, except that the lower limit of sex distinction does not occur at a definite length. Unsexable specimens shown by the vertically hatched area, immature males and females by black areas, and mature males and females by obliquely hatched areas.

females (Fig. 7). At all times more males than females were mature, probably because of their much smaller size. For all specimens the ratio was 1 mature male:0·374 mature female. As in all species the number of eggs per female varied widely from 1 to 109 (mean number 33·3), and the number increased generally with the size of the females as follows:

Length of female (mm)	5½–6	6–6½	6½–7	7–7½	7½–8	8–8½	8½–9	9–9½	9½–10
No. of specimens	3	43	58	60	37	17	1	2	2
Mean no. of eggs	21·3	25·0	29·0	31·2	41·7	54·4	62	66·0	108·5

As in *G. pulex* there was no indication that in any one size-group the number of eggs per female showed any seasonal variation. Embody (1911) found in New York State a higher average number of eggs (45) but some of his females were over 11 mm long. He also found the species breeding in a wide range of temperature (6–30° C) and thought it possible that it bred all the year round. He had, however, no samples for October, November and December.

Crangonyx gracilis does not perform precopula; it would indeed be impossible because the male is so much smaller than his mate. The females become attractive to the males just before they moult. The males remain near such a female and jostle one another. Mating occurs after the female moults, and closely resembles that described in

Orchestia gammarella (Pallas) by Williamson (1951). The female lies on her side while the male lies across her and holds her with his gnathopods at the 3rd–4th and 5th–6th thoracic intersegmental membranes while his antennae are clasped round her body. They remain in this position for about 10 min, during which time the female may swim along on her side. The female then breaks away, and she lays her eggs within about 4 h. The absence of any cycle in the field makes it impossible to infer anything about the life-history of the individual as has been done for *Gammarus* spp. Embody (1911) gives a few facts, although he was not successful in breeding the species in the laboratory. He found that incubation took eight days at 23° C and that the young matured and grew very slowly and were not mature after 13 moults at an age of 124 days. He does not state the sex of his individuals, nor does he mention the disparity in size of the sexes.

My own laboratory observations, which were more successful but less detailed, gave the following results. Incubation took 48 days (2 specimens) at an average temperature of 3·5° C and 14–17 days (average 15·3, 7 specimens) at an average temperature of 15° C. The young took a very long time to mature at room temperature (*c.* 10–20° C) and within each batch of young there was extraordinarily great variation. The males matured first, after 4–14 weeks (average 7·8, 13 specimens), and the females after 16–36 weeks (average 26·5, 8 specimens), and some specimens appeared to take even longer. For instance, two sisters of the female who was mature after 36 weeks died later and were still immature. The difference in average time taken to reach maturity in the two sexes accounts for the sex ratio phenomena discussed above. The shrimps bred readily in the laboratory in water from the River Dee, but not so well in Liverpool tap water, where many clutches of eggs failed altogether, and even when they did not, few young were produced. When young the females bred continuously, laying and moulting almost as soon as their young were hatched, but as they aged the intervals between broods became longer, and they often passed through periods of a few weeks when no eggs developed in their ovaries. Six pairs of laboratory-reared specimens were kept under observation till they died, and when one partner died a substitute was provided. The females laid 4, 4, 5, 6, 7 and 8 batches of eggs, and lived for 10, 17, 15, 12, 14 and 19 months, and the males lived for 11, 14, 13, 14, 17 and 21 months. There would therefore seem to be little difference in the length of life of the two sexes, although the males mature much earlier.

It is apparent, therefore, that with the long and very varied time taken to reach maturity, the long period of breeding and the fact that breeding can occur at all seasons there would be no annual variation in the structure of a wild population, and this was found to be so.

DISCUSSION

With the data obtained in this and a previous (Hynes 1954*a*) study, it is possible very roughly to calculate the biotic potential of the various freshwater species under British conditions. If one considers a single female who becomes sexually mature on or as soon as possible after 1 January and survives her full span, one can obtain some idea of the potential number of her offspring on 31 December.

G. pulex will produce young in early March, mid-April, early May, late May and

mid-June and she might produce a further brood before her death. She will average about 16 young per brood, and the first brood containing six or seven females (fewer than average as she will then be a small female) will have time to produce at least one and probably two broods each before the onset of the resting period. The total number of her offspring will therefore be at least of the order of 200–300.

G. lacustris will produce young in mid-April and then possibly three or four more broods averaging 22 eggs before her death in June or July. She will at prevailing temperatures not have time for more than this, and none of her offspring will mature before the end of the year. Her production will therefore be of the order of 100 offspring, or less.

G. duebeni in a freshwater stream (Hynes 1954*a*) will produce young in mid-February, late March, late April and late May. To have matured soon after 1 January she must have been born about April, so she might have time for a further brood before her death at 15 months. Her average clutch will be about 19 eggs in fresh water and none of her offspring will mature in time to produce young before 31 December. Her production will therefore be of the order of 100 offspring or less, although it will be of greater potential value that that of *G. lacustris* because about two-thirds of the young will be females. This species has a peculiar sex ratio. Kinne (1953*d*) gives figures which are considerably higher than this, and are of the order of 200, but he was concerned with a brackish water population which lays more eggs (Hynes 1954*a*) and lives at much higher summer temperatures. This gives time for the production of six broods.

G. fasciatus will lay eggs in March, but the first clutch may fail; young will be produced in mid-May and there will be time for perhaps two more clutches before her death in July. Her clutches will average 29 eggs, and possibly all broods will produce one or even two or three clutches of eggs before the resting period begins in October. Her potential number of offspring is therefore very high, and may be of the order of 1500 on 31 December.

Crangonyx gracilis also has a high potential reproduction rate. She will produce young, averaging 33 per clutch, in mid-February, mid-March, mid-April, early May and mid-May. Of these the first clutch (about 15 females) will breed three times before the end of the year, the second twice and the third once. This gives a figure of the order of 3000 offspring by 31 December.

These figures are admittedly only very rough approximations, but it seems probable that they have some validity. It has been shown earlier (Hynes 1955) that on zoogeographical grounds there are reasons for supposing that, in Britain, *Gammarus pulex* is an ecologically dominant species, and it would seem that differences in biotic potential will to some extent explain why this should be so.

G. pulex can inhabit both streams and lakes, which are the normal habitats of *G. duebeni*, and *G. lacustris* respectively, although the former also occurs in Irish lakes. Assuming that these three species make more or less the same demands on the habitat, it is to be expected that, because its biotic potential is at least twice that of the other two species, *G. pulex* will ultimately oust them from any habitat to which it obtains access. If one adds to this the fact that *G. duebeni* in fresh water is apparently more stenotopic than *G. pulex* (Hynes 1954*a*, 1955) one can understand why it is that,

on the whole, when *G. pulex* has been present on any land mass for a considerable time *G. duebeni* is completely absent from fresh water. In contrast, *G. lacustris*, although confined to lakes, is more resistant to low oxygen content and generally stagnant conditions than *G. pulex*, as is immediately clear from the differing ease with which the two species can be kept in captivity; this has also been noted by Kaiser (1941). This species has, therefore, in some lakes refuges in which it is free from competition (Hynes 1955), and is therefore, unlike *G. duebeni*, sometimes found with *G. pulex*. As already noted above (p. 370) *Polymorphus minutus* may aid in the elimination of *Gammarus lacustris* from lakes in which it might otherwise withstand competition with *G. pulex*. *G. duebeni* and *G. lacustris* appear to differ little in biotic potential, and they are known to occur together in some Irish lakes (e.g. L. Erne and L. Gara, Sligo). Possibly they differ sufficiently in their ecological requirements to facilitate co-existence. No detailed study of such habitats has been made. The same possibly applies to *G. duebeni* and *G. fasciatus*, which both occur in L. Neagh and the R. Bann. Dr Macan, who collected both these species in L. Neagh, reported that the two stations where he found *G. fasciatus* were off sandy low-lying shore somewhat fouled by cattle, whereas the station where he found *G. duebeni* was a shore of fixed boulders and gravel.

Crangonyx gracilis with its high biotic potential would be expected to be able to hold its own against *Gammarus pulex*, and the two species are in fact sometimes found together. It has, however, somewhat different microhabitat requirements from *G. pulex*, as it inhabits weedy places and deposits of vegetable debris, whereas, on the whole, *G. pulex* is found in cleaner habitats. It would, however, seem possible that *Crangonyx gracilis* may become the dominant form in some types of habitat (e.g. watercress beds and silty streams with rooted vegetation) which are at present inhabited by *G. pulex*. It is, of course, possible that the latter has some other ecological advantage which offsets its lower reproduction rate, but this is not at present apparent.

G. fasciatus remains a problem. It clearly has a high biotic potential because of its rapid rate of growth, but despite this it is, in England, almost confined to peculiar saline habitats, although in Ireland it occurs in fresh water. It also can inhabit loci which are clearly unsuitable for *G. pulex*, being found in weedy places and on muddy substrata. It may be that, being adapted to a different climate it can here realize only a very small fraction of its biotic potential, but this does not account for its absence from localities which are unsuitable for *G. pulex*. It occurs in the canal at Coventry, and so, like *Crangonyx gracilis* (Hynes 1955), has access to much of England. It may be that some biotic factor, other than *Gammarus pulex*, prevents its spreading into fresh water in England but not in Ireland. It apparently suffers greatly from predation even at Frodsham, probably mostly from dragonflies and sticklebacks. These animals are usually abundant in weedy muddy places, and it may be that only where they are absent or scarce, i.e. in places suitable for *G. pulex* also, can *G. fasciatus* establish itself in quite fresh water. If this is so, it might account for the peculiar distribution which has been observed. At the time of writing the species seems to be satisfactorily established in fresh water in an aquarium with dense weed and a muddy substratum but without predators. Possibly this problem could be solved by suitable field experiments.

The resting period through which several of the species pass is of considerable interest. Kinne (1953*b*) has shown that in females of *G. duebeni* in brackish water its onset is apparently caused by falling temperatures. It would seem that the same is probably true of *G. pulex* also (see above). *G. duebeni* in fresh water does not show this phenomenon, and it has been suggested (Hynes 1954*a*) that this may be because of the low summer temperatures in the freshwater habitats in which this species occurs. Probably falling temperatures cause the onset of the resting period in *G. fasciatus* also. All attempts, however, to induce it experimentally during the summer, by placing specimens in a cold room, failed. In *G. pulex* and *G. fasciatus*, males as well as females show morphological evidence of the suspension of sexual activity, and it is particularly interesting that in both these species this begins and ends earlier than that of the females (Tables 1–3 and 6). In *G. pulex*, and in *G. duebeni* in brackish water, the resting period ends during the coldest period of the year and before midwinter, so the stimulus which initiates breeding would seem to be neither temperature change nor day-length. In *G. fasciatus* also some males re-acquire curly hairs before midwinter and during the coldest season (Fig. 4), but the females do not begin to lay eggs until March (Table 6), although a single ovigerous specimen was found in January 1954. It may be that here also the end of the resting season is determined neither by temperature nor day-length, but if that is so it is strange that no breeding occurred in the large laboratory tank before the end of April (p. 376). This may, however, have been due to shortage of animal food. During the early months of this experiment the mud had been full of Tubificidae, and during March it was noticed that these had all disappeared. Animal food was then supplied in the form of chopped *Tenebrio* and dead fish, and ovigerous females appeared within a few weeks. The whole resting period in the tank may therefore have been due to shortage of animal food, and so not comparable with that in the field. Clemens (1950) found it necessary to feed this species on meat in the laboratory, and it seems probable that the difficulties I experienced when keeping the shrimps under close observation were due to inadequate diet. The resting period therefore apparently begins because of falling temperature, and lasts for a short period in *G. pulex*. It seems probable that the same thing may be found to apply to *G. duebeni* in some freshwater habitats where summer temperatures are higher than in the small streams investigated (Hynes 1954*a*). The shortness of the resting period in *G. pulex* would seem to be an adaptation to the mild winter of western Europe. It would, however, be very instructive to know how long this period is in the climatically more severe region of southern Sweden, where the species also occurs (Stålberg 1940). In *G. fasciatus*, which is adapted to the long hard winter of North America, the resting period is longer. In *G. lacustris* a similar adaptation to climate can perhaps be detected. In this species growth to maturity is so slow that no resting period occurs, but the breeding period is very short and concentrated. This species occurs in the far north of Europe, where summers are short, and such a life-cycle would appear to be admirably adapted to such conditions. Finally, *Crangonyx gracilis* has been found to show no breeding cycle of any kind. It may be that in this country the annual fluctuation of temperature is too small to affect it, but it would seem from Embody's (1911) observations that it also breeds continuously in its native land.

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SUMMARY

1. The life-cycles of *Gammarus pulex pulex* (L.), *G. lacustris* Sars, *G. fasciatus* Say and *Crangonyx gracilis* Smith were studied by means of size, sex and sex-condition analyses of random samples collected from single localities at regular intervals throughout a year. From these the sequence of the generations, rate of growth, number of batches of eggs laid, etc., were deduced. Samples of *G. pulex* and *G. fasciatus* were collected from other localities to determine if the same cycles of events occurred elsewhere.

2. Observations were made on shrimps in the laboratory to confirm or elucidate various points in the life-cycles.

3. It is shown that infection of *G. lacustris* with the acanthocephalan *Polymorphus minutus* (Goeze) causes sterility, and it is suggested that this may be a disadvantage to this species, as compared with *G. pulex*, because it is confined to lakes.

4. *G. pulex* and *G. fasciatus* are shown to pass through a winter period when no breeding occurs, and adults lose some of their secondary sexual characters. The ecological implications of this resting period are discussed.

5. With the data obtained, and those obtained on *G. duebeni* Lillj. in a previous study, the biotic potential of the five species of amphipod occurring in British fresh waters are worked out. It is suggested that the greater biotic potential of *G. pulex* accounts at least in part for its apparent ecological dominance over *G. duebeni* and *G. lacustris*.

6. It is suggested also that *G. fasciatus* is, in this country, not able to realize its potentially high reproductive rate, and that this fact, and predation, probably account for its peculiar distribution in the British Isles.

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THE FLIGHT ACTIVITY OF THE SYCAMORE APHID, *DREPANOSIPHUM PLATANOIDES* SCHR. (HEMIPTERA, APHIDIDAE)

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The flight behaviour of aphids is equally interesting in species which keep to one host as in those which change between primary and secondary host during their life. The work of Moericke (1941), Broadbent (1949), Kennedy (1950), Müller (1951), Müller & Unger (1951), C. G. Johnson (1954), Haine (1954) and B. Johnson (1954) among others has thrown some light on the alighting and take-off behaviour of aphids of economic importance, e.g. *Myzus persicae* Sulz., *Aphis fabae* Scop. and *Brevicoryne brassicae* L. Although we know little about the length, direction, distance and maintenance of flight in these species, it is clear that in certain aphids flight is necessary before reproduction can begin on a larger scale and that the flight muscles then degenerate. Further flights thus become impossible.

Since differences in behaviour are to be expected between aphid species which alter their host plant throughout the seasonal life-cycle and those which do not, it would be interesting to know how those tree aphids which do not alter their host behave in first and repeated take-off under different environmental conditions, and how long they maintain flight during their life. In wind-tunnel experiments species from sycamore, lime, oak and spruce showed less tendency to take off in relatively higher wind-speeds than *Aphis fabae* and *Brevicoryne brassicae* (Haine 1954, 1955). Nevertheless, there were a few starts in 4–5 m.p.h. by *Drepanosiphum platanoides* Schr. and *Periphyllus aceris acericola* Wlk. on their 5th and 2nd day respectively after last ecdysis, by *Eucallipterus tiliae* L., *Tuberculoides annulatus* Hartig and *Cinaropsis pilicornis* Hartig of unknown age on their 5th, 4th and 3rd day respectively after collection. But these exceptions occurred in spring and there was no evidence that it was generally repeated throughout the summer. These aphids behaved in much the same way as *Aphis fabae* in that they preferred the lower wind-speeds to the higher, and took off regularly from the exposed parts of the leaves against or diagonally into the direction of the wind, often after many trials. Although they responded rapidly when wind-speed changed from high to low they were less ready to take off in lower speeds of 2–3 m.p.h. than *A. fabae*. Despite this they were able to take off and fly in calm air after astonishingly long periods.

A. fabae was found to start in 5·8 m.p.h. on its 5th day after last moult after 3 days' previous flight exercise, and up to its 7th day in calm air. *Phyllaphis fagi* did not take off in relatively high speeds at all, but flew well on its 12th day in calm air. *Euceraphis punctipennis* flew on its 16th day after collection. Single alatae of *Drepanosiphum platanoides* proved able to fly on their 20th day.

Special attention was paid to this last species and its flight activity observed in greenhouse experiments and in the field. In preliminary tests it could be demon-

strated that alatae (*c.* 50) collected from trees, flew almost until their death. Voluntary flight, lasting for several minutes, was observed on the 13th day and even later, the characteristic leap from the undersurface of the leaf and subsequent flight after disturbance on the 27th, and in a single case on the 36th day after collecting the material. Though the exact age of these alatae was not known there could be little doubt that early flight muscle autolysis as recently demonstrated for *Aphis fabae*, *Myzus persicae*, etc., by B. Johnson (1954), did not occur in the life of these tree aphids.

Detailed observation on *Drepanosiphum platanoides* (*c.* 45) of known age so far allows us to state that summer virginoparae and sexuparae fly readily until their 50th and 70th day after the last cast of skin, i.e. until shortly before they died. This extraordinarily extended flight has not been recorded for an aphid before. The ability to fly is lost progressively during the last week of life. At the beginning of this process the alatae become unable to fly upward, then able to use the wings only for a spirally directed downward flight, finally only to use the wings as sails when they are held out passively. As one might expect in a natural population the percentage of alatae able to fly was always relatively high. This can be seen from the following few examples of continued observations:

4 Aug. 1954	17·45	100 %	From 41 alatae
5 Aug. 1954	10·20	84 %	From 50 alatae
5 Aug. 1954	15·45	85 %	From 58 alatae
11 Aug. 1954	15·00	90 %	From 60 alatae

Apart from the fact that early flight muscle autolysis does not occur in *D. platanoides* (and probably *Euceraphis punctipennis*), the flight behaviour differs from that of *Aphis fabae*, etc., and therefore merits a short note. Special attention was paid to the question whether *Drepanosiphum platanoides* having reached flight maturity within 24 h would take off from the leaves and leave the tree in straight upwards directed flight as has often been observed for bean- and potato-aphids (compare C. G. Johnson 1954, Haine 1954). Though the observations started as early as 12 May, when spring alatae had just appeared, and though all hours of the day were covered, the characteristic first start and flight away from the breeding host into the brightest light was never clearly observed. On the contrary these alatae with great regularity kept within about 0·5–1·5 m of the tree or of its branches. The direction into the brightest light was obviously avoided and the rare departures away from the tree, actually observed in single individuals throughout May until September, were directed towards another group of trees or a dark wall of coniferous or yew trees, or towards hedges and shrubs.

A few data from continued observations (Table 1) will demonstrate how this well-directed flight is linked with a marked preference for calm air. Flight activity occurred with great regularity, especially during the late afternoon (1700–1800 B.S.T.) until evening (2000–2100 B.S.T.) in a fairly wide range of temperature (13·5–21·5° C), relative humidity (65–88 %) and daylight (from bright sunny afternoon to dim dusk), but scarcely without any exception in calm air. Unfortunately there were no completely calm days, which would have enabled one to judge to what an extent this activity, which Theobald (1927, p. 387) describes as the characteristic 'hovering' around the trees, is maintained in calm conditions throughout the day, or whether it

is confined to the later afternoon and evening in which other aphids showed special moulting and reproductive activities as well (Haine 1954, and in preparation). Lack of light rather than low temperatures and high relative humidity almost certainly plays an important part as the flight-limiting factor in the late evening. For the great skill of this evening flight seems to be indispensably bound to light and the big night catches of *D. platanoides*, recorded by Eastop (1951) occasionally, are apparently due to this evening flight activity.

Table 1. *Flight activity of* Drepanosiphum platanoides *on* Acer pseudoplatanus, *Rothamsted Park, 1954*

	Time (B.S.T.)	Temp. (° C)	R.H. (%)	Wind	Flights
5 Aug.	1020	17	73	Windy—gusty	Infrequent
	1100	17	86	Windy—gusty	Infrequent
	1500	18·3	78	Slightly windy	Infrequent
	2045	16·5	78	Slightly windy	Infrequent
15 Aug.	1955	14	73	Calm	Plenty
	2015	14	83	Calm	Many
	2025	13·5	88	Calm	Several
	2100	13·5	91	Calm	None
27 Aug.	1430	22	63	Slightly breezy	Infrequent
	1700	22·5	53	Slightly breezy	Infrequent
	1930	17·5	70	Calm	Plenty
28 Aug.	0900	15·5	72	Calm—slightly breezy	None
	1100	17	72	Calm—more steady breeze	Infrequent
	1300	18·3	62	Calm—more steady breeze	Infrequent
	1640	21	60	Slightly breezy	None
	1840	18	65	Calm	Several
	1915	16·3	70	Calm	Several
31 Aug.	0900	15	76	Slightly breezy	None
	1115	18·5	75	Slightly breezy	None
	1300	21·6	68	Calm—slightly breezy	Very infrequent
	1500	24	60	Calm—slightly breezy	Infrequent
	1630	25·5	43	Slightly breezy	Very infrequent, quick
	1825	21·5	66	Calm	Several
	2000	18	73	Calm	None

The take-off from the upper surface of the leaves was less frequently observed than the take-off from the lower surface by means of a leap. Weber (1930), Rietschel (1952) and Quednau (1954) have already pointed out that the structural modification of the front legs into spring-legs enables *Drepanosiphum* virginoparae and sexuparae as well as their fundatrices and males to leap back and downwards from the undersurface of the leaves immediately into flight. They share the ability to jump with other species of the subfamily Phyllaphidinae, among which *Eucallipterus tiliae* was found to leap less readily than *Drepanosiphum platanoides* while *Euceraphis punctipennis* seemed to jump in a more nearly horizontal direction. The distance of leaping, which for *Drepanosiphum platanoides* tended to be 20–30 cm during the morning, reached 40 cm easily during the late afternoon when general flight activity was noticed.

More skill, however, seemed to be developed in the alighting process. In several hundred single observations *D. platanoides* was found to alight in 40–60 % of all cases

on the upper surface, in 20–30 % on the lower surface, in 5–10 % on leaf edges and 2–5 % even on the stems of the leaves. This alighting, precisely performed in different flight speeds on very inconvenient parts of the host plant, could not be carried out without reliable means of gripping. Instead of the characteristic aroliar pads or pulvilli the leaping species are provided with strong spines (differing in number and size and sometimes movable) at the distal end of the tibiae which in *Drepanosiphum* end transversely allowing the tarsi to swing out completely. Thus the spines seem to serve both for holding and for taking off, and their interaction with the tarsi is apparently more important in the operation of alighting than in that of taking off.

The flight of *D. platanoides*, a species which maintains alatae throughout all seasonal generations, is as easy and elegant as the alighting. Whatever the direction and speed it seems well controlled. Even a slow vertical flight up and down is achieved. The lightness of this flight in connexion with a perfectly controlled alighting, hardly surpassed by any other insect, may well justify a comparison with a helicopter. The speed of flight has not been recorded, but it was scarcely higher than in other species of similar size and increased obviously during warm early afternoon hours when single individuals performed a short quick zig-zag flight within the tree. The usual duration of flight of the virginoparae, observed round the tree, amounted to 5–15 sec, scarcely exceeding 40 sec. An aphid often took off again very soon after alighting.

Though these observations indicate an exclusive association of *D. platanoides* to its host, single actively migrating individuals in the air, many yards away from the next sycamore tree, have been observed throughout the season. In suction trap and sticky trap catches migratory flight of *D. platanoides* has also been recorded by Johnson & Eastop (1951) and Broadbent & Doncaster (1949) and it is most likely that these migrations were built up by occasional departures from the tree, mentioned before, but it has still to be found out whether there are certain circumstances under which they take place and whether they can occur at any stage of adult life, for which a few experiments provide some evidence: after a short initial flight trial on the 7th day and no further flight in between, single sexuparae were able to take flight voluntarily on their 64th day after the last ecdysis. First active take off and flight was also observed in six sexuparae on their 24th–30th day after the last moult without previous flight exercise.

The reproduction of virginoparae and sexuparae alatae, which were kept on isolated small trees, started earliest on the 5th to the 6th day after the last ecdysis, in many cases noticeably later. The rate was low and did not exceed 0·1–1·2 larvae per day. The measurements of a newly born larva in comparison to the alata producing it were (in a single case: length 0·91 mm: 2·26 mm; width 0·41 mm: 0·75 mm) relatively high, which seemed to indicate that the development of embryos into birth stage takes place singly. But more information is required on this point. The results of flight experiments so far suggest that reproduction does not appear to be directly influenced by flight activity as it was shown to be in *Aphis fabae* by B. Johnson (1954). There is no evidence that reproduction is inhibited in alatae without flight exercise nor increased in alatae with flight exercise.

DISCUSSION

The observation that *Drepanosiphum platanoides* does not lose its ability to fly by autolysis of the flight muscles is of systematic as well as biological interest. A discussion on the extraordinary flight activity maintained by *D. platanoides* in a locally restricted area throughout life should not be attempted without reference to the flight activity of other aphid species. So far it can be stated that *D. platanoides*, as well as *Euceraphis punctipennis*, which was found to fly well on its 30th day after collection, and *Phyllaphis fagi*, do not autolyse their wing muscles, at least not up to a considerable age. There is also evidence that *Eucallipterus tiliae* and *Tuberculoides annulatus* do not lose their ability to fly at an early stage. But whether this is a general feature of the subfamilies Phyllaphidinae and Callaphidinae, or whether it is restricted to their representatives with winged generations only, has still to be examined.

We have to consider whether early flight muscle autolysis is a secondary stage in aphid evolution and whether it might occur in aphids of a primary stage as well. It is possible that there are species with intermediate stages which lose the ability to fly later in life or in certain individuals or generations only, and we are interested to know whether this occurs under special circumstances. More knowledge on this matter might enable us also to recognize the biological importance of the loss of ability to fly in one species and its maintenance in the other.

In contrast to *Aphis fabae* (C. G. Johnson 1954, Haine 1954) which is characterized by regular departures within the first few days from the breeding host even under unfavourable weather conditions (wind-speed up to 5–7 m.p.h.), by large-scale migration mainly achieved by passive wind-transport and followed by early flight muscle autolysis, *Drepanosiphum platanoides* is characterized by rare departures from the breeding host, but unlimited flight activity throughout its lifetime and continued active distribution by short purposeful flights within the host. *D. platanoides*, moreover, is distinguished by a highly specialized take-off and alighting ability, and an extraordinarily developed flight skill, for which there is no parallel in *Aphis fabae*.

It is interesting to see that these species have also developed different reproductive schemes. *A. fabae*, *Myzus persicae* (Fenjves 1945), and *Brevicoryne brassicae* alatae (Markkula 1953) are characterized by a relatively high reproduction at the beginning and a reduced and unreproductive phase afterwards; *Drepanosiphum platanoides*, on the other hand, by a late beginning and low but constant rate throughout its lifetime.

It seems that *Aphis fabae*, after its migratory flight, tends to make quick and best use of suitable but physiologically rapidly changing summer host plants by means of an early concentration of reproduction and early loss of flight ability, which might lead to a certain accumulation of growing colonies and finally to overcrowding. *Drepanosiphum platanoides*, as an excellent flyer, continuously on the move at least throughout certain hours of the day during its lifetime, is most unlikely to do so. On the contrary, its largely extended flight activity in connexion with a low rate of reproduction seem to enable its generations to maintain a loose distribution over its host, for which it shows a true adaptation in the sense of Kennedy, Ibbotson & Booth (1950, p. 678). Its quickness and readiness to take off by means of a leap from the undersurface of

the leaves will also enable it to escape most skilfully its parasites and predators, among which spiders play an important part.

More information is required before we can distinguish between different biological tendencies, indicated by the different flight and reproductive activities in the species. These can hardly be understood unless the species are seen in the complexity of their relations with their host plants and natural enemies.

SUMMARY

The take-off, flight and alighting behaviour of *Drepanosiphum platanoides* Schr., maintaining alate generations on sycamore throughout the season, are described. Though departures from the breeding host were scarcely observed, virginoparae and sexuparae alatae proved able to fly until shortly before they died, indicating that early flight-muscle autolysis does not occur in this species. This great extension of flight activity throughout lifetime was connected with a low daily rate of reproduction.

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THE LARGER INVERTEBRATE FAUNA OF THREE RABBIT CARCASSES

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(With 2 Figures in the Text)

During a university entomology course held at the Juniper Hall Field Centre, Dorking, in 1951, daily investigations were made for two weeks by a group of students* on the larger invertebrate fauna of three rabbit carcasses. In the evening of 4 July three freshly killed rabbits were put out in places separated by approximately 30 and 40 m. Carcass (A) was placed just inside a small shrubbery with no undergrowth and amongst partly rotted leaves. This habitat was generally dry and in deep shade. (B) was placed on cinders in loose sward under a large plane tree; this habitat was more subject to early morning dew than (A) and was exposed to light. (C) was situated in thick grass near the open verge of a meadow. Each carcass was covered with wire-netting pegged down at the corners to prevent disturbance by foxes and dogs. During examination this netting was removed and the carcass in each case was disturbed. Daily observations were made between 0800 and 0830 h G.M.T., 5–18 July inclusive. In many cases it was necessary to collect specimens for identification. In only a few instances did specimens escape unrecorded, and these represent only a fraction of the fauna present on examination. Not all specimens seen or caught have been fully identified, but specific determinations have been undertaken where possible. Grateful acknowledgement is made to the members of the staff of the Brit. Mus. (Nat. Hist.) who came to our aid with the more difficult species.

LIST OF SPECIES OBSERVED

Mollusca
Pomatias elegans Mull. and other species.

Isopoda
Armadillidium sp. and other species.

Arachnida
Araneida
Acarina

Insecta
Dermaptera
Forficula auricularia L.

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INSECTA (*cont.*)
HEMIPTERA
Nabis lativentris Boh. and other species.
COLEOPTERA
Carabidae
Harpalus rufipes (Deg.)
Pterostichus niger
Hydrophilidae
Cercyon lateralis (Marsh.)
C. unipunctatus (L.)
Silphidae
Necrophorus humator (Goeze)
N. vespillo (L.)
Thanatophilus rugosus (L.)
T. sinuatus (F.)
Ptomophagus subvillosus (Goeze)
Catops fuscus (Pz.)
C. kirbii (Spence)
Staphylinidae
Oxytelus sculpturatus Gr.
Philonthus laminatus (Cr.)
P. fuscipennis (Man.)
Creophilus maxillosus (L.)
Tachinus rufipes (Deg.)
Aleochara curtula (Goeze)
Histeridae
Saprinus semistriatus (Scrib.)
Hister striola Sahl.
H. cadaverinus Hoff.
H. carbonarius Hoff.
Cantharidae
Metacantharis clypeata (Ill.)
HYMENOPTERA
Braconidae
Alysia manducator (Panz.)
Cynipidae
Figites laevigatus Dahl.
Formicidae
Myrmica laevinodis Nyl. and other species.
Vespidae
Vespula vulgaris (L.)
DIPTERA
Therevidae
Thereva sp.
Piophilidae
Piophila varipes Meigen
P. foveolata Meigen
Sphaeroceridae
Limosina luteilabris Rond.
Calliphoridae
Sarcophaga sp.
Calliphora sp.
Lucilia sericata (Meig.)
Muscidae
Hydrotaea armipes (Fallen)
Fannia scalaris (Fabr.) and other species.

Of previous work on the insect visitors to carrion, a large proportion was concerned with the blowfly problem in sheep-rearing areas of Australia and South Africa. Any attempt to obtain quantitative data on blowfly numbers was clearly beyond the scope of this work, but rough estimations of numbers of other insects were obtained without introducing too great a degree of artificiality into the observations. It was not found possible to collect and breed out the insects on the completion of the observations.

Fuller (1934) recognized three stages of decomposition of carcasses:

(1) In which the freshly killed host was not smelling strongly.

(2) Beginning when active liquefaction and disintegration became noticeable. Characterized by a strong smell and the frequency of dipterous larvae and Coleoptera.

(3) The drying of the carcass with loss of smell.

In the carcasses the onset of the second phase began in all cases on about the fourth day, with reduction of the numbers of larvae on A and C beginning on the 7th day. In both these cases the third, drying, phase was apparent by the 9th day. In the case of B, however, the second phase continued from the 4th until at least the 14th day.

Assuming that all the carcasses were equally accessible to the blowflies for egg laying, a reasonable assumption, having regard to the work of Gilmour, Waterhouse & McIntyre (1946), the causes of these major differences may be due either to differences in the associated insects or to the different effects of varying microclimatic conditions.

The proximity of the three carcasses to each other was such that there was no reason to assume that they were accessible to distinct faunas except in so far as these were affected by the microclimate.

The carcass A was in shade and thus protected to some extent from external moisture while, conversely, its position was such as to keep the temperature low and evaporation rate low. B was more exposed to the atmosphere and thus subject to wetting by dew and rain but also to higher temperature and a higher evaporation rate. Further, this carcass was on cinders so that the surface moisture was rapidly drained away from it. C was in long, damp grass and so was perpetually wet but at the same time in no way shaded from the sun. The high temperature and humidity conditions at C were, perhaps, optimal for decomposition, while those at A were similarly damp but rather cooler. B, on the other hand, was subject to drying in the daytime but the constant wetting by dew and rain kept the carcass in an available condition for fly larvae for much longer than was the case with the other two carcasses. Because of this extension of the second phase B was far more productive of insects than either of the other carcasses and most of the following observations refer to this carcass.

The insects visiting the carcasses fall into two groups: those scavenging on the carcass itself and those parasitic or predaceous on the dipterous larvae. By far the most important scavengers were the dipterous larvae themselves. Adult Diptera were observed at all the carcasses on the 1st day and larvae were first seen on the 3rd, 4th and 5th days on B, C and A respectively. A drop in numbers of larvae in A and C was noted after the 6th day. This possibly resulted from the intense competition between the larvae, and as such the drop resembled that figured by Holdaway (1930), but was no doubt also due to some numbers of the larvae leaving the carcass to pupate, since the larvae of *Lucilia sericata* mature in about three days from hatching (Ullyett 1950) and migrate away from the carcass to pupate.

Other scavengers included the Diptera *Piophila* spp. and *Fannia scalaris* with scavenging larvae. Fuller (1934) and Myers (1929) regard *Piophila casei* (L.) as a late arrival, but in the present case *P. varipes* was seen on the 3rd day and Duffield (1937) records this and three other species of *Piophila* from carcasses stated to be 4 days old. Illingworth (1927) first records *P. casei* on the 3rd day of an experiment but it was most frequent after 6 days. From the description given it appears that by this time the second phase of decomposition was giving way to the third so that the carcasses were in an advanced state of decomposition. This brings out the importance of describing the state of decomposition, even if only using such simple criteria as smell and frequency of dipterous larvae, in addition to the age of the carcass. Clearly under different conditions of climate and accessibility the rates of decomposition will vary considerably so that the age of a carcass is not of great significance.

Additional scavengers were the ants and wasps, although the wasps might equally well have been predaceous on the fly larvae. The beetles of the families Silphidae and Histeridae may also have been either scavengers or predators, but opinions are divided as to their effects on the fly population. Holdaway (1930) regards the Histerids as important in the reduction in numbers of blowflies but, according to Salt (1932) the only factor of any importance in this respect is competition between the blowfly larvae themselves. Fuller sums the matter up adequately as follows, '...it is the

surplus of maggots, forced off the carcass before completing their development, which is seized and destroyed by the waiting predators. This surplus would otherwise have succumbed through starvation; consequently the beetles play no part in regulating the blowfly population.'

The commonest Histerid found during the observations was *Saprinus semistriatus* which did not appear at corpse B until the 4th day (Table 1 and Fig. 1). The numbers of this beetle remained relatively constant from the 6th day onwards except for a drop on the 9th and 10th days which were quite cold. This beetle was feeding on the dipterous larvae and this is correlated with its non-appearance until the latter were well established and also with its later constancy in numbers.

Table 1. *Summary of the more prominent insects visiting carcass B*

Arranged in families in order of appearance. Dipterous ova and larvae are indicated as present or absent.

	Day													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Coleoptera														
Aleochara curtula	–	–	10	10	35	45	55	50	25	15	12	10	1	1
Necrophorus vespillo	–	–	–	1	1	–	–	–	–	–	–	–	–	–
Pterostichus niger	–	–	–	1	–	–	1	–	–	–	–	–	–	–
Saprinus semistriatus	–	–	–	1	6	19	20	20	15	5	20	20	15	18
Necrophorus humator	–	–	–	–	1	–	4	–	–	–	–	–	–	–
Hister cadaverinus	–	–	–	–	1	–	–	8	1	5	3	–	–	5
Creophillus maxillosus	–	–	–	–	–	–	2	2	–	1	3	1	–	5
Hister striola	–	–	–	–	–	–	–	1	1	–	1	1	2	1
Ptomophagus subvillosus	–	–	–	–	–	–	–	1	–	–	–	–	1	1
Thanatophilus sinuatus	–	–	–	–	–	–	–	–	1	2	1	1	–	–
T. rugosus	–	–	–	–	–	–	–	–	–	1	1	–	–	2
Philonthus laminatus	–	–	–	–	–	–	–	–	–	1	1	–	–	–
Hymenoptera														
Alysia manducator	–	–	–	2	5	5	–	5	–	–	–	–	–	–
Figites laevigatus	–	–	–	–	–	–	–	–	–	3	–	–	5	5
Vespula vulgaris	–	–	–	–	–	–	–	–	–	–	–	1	1	1
Diptera														
Calliphora sp.	5	2	5	–	–	–	–	–	–	–	–	–	–	–
Lucilia sericata	–	–	5	10	4	–	1	5	–	5	5	20	15	5
Sarcophaga sp.	–	–	–	10	4	–	1	10	5	5	5	–	–	5
Fannia scalaris	–	–	–	–	–	–	12	10	–	5	5	5	5	5
Ova	–	–	+	+	+	–	–	–	–	–	–	–	–	–
Larvae	–	–	+	+	+	+	–	+	+	+	–	+	+	+

The only undoubted scavengers among the Coleoptera were the *Cercyon* spp. and possibly some of the Staphylinids. The commonest Staphylinids were *Creophilus maxillosus* and *Aleochara curtula*, the latter being the most abundant beetle of all. *Creophilus maxillosus* is predatory in both larval and adult stages while *Aleochara curtula* is an obligate parasite of dipterous pupae and the adults feed on the fly larvae. *A. curtula* first appeared on the 3rd day (Fig. 1). Numbers rapidly increased until a maximum was reached on the 7th day after which they fell off equally rapidly. Wadsworth (1915) states that the adults of *A. bilineata* copulate within three days and then burrow in the ground. It appears that this is also true of *A. curtula*, the marked decline in numbers noted on the 9th day being four days after its arrival in any

numbers. The numbers of *A. curtula* recorded were considerable and, acting at a time when many hazards are past for the dipterous larvae, may well be of some importance in the reduction of blowflies.

The burying beetles, *Necrophorus* spp., first appeared on the 4th day and were last seen on the 7th. They made no progress in burying the carcass because of the disturbances caused by the daily observations. Walsh (1931) and Kaufmann (1941) give

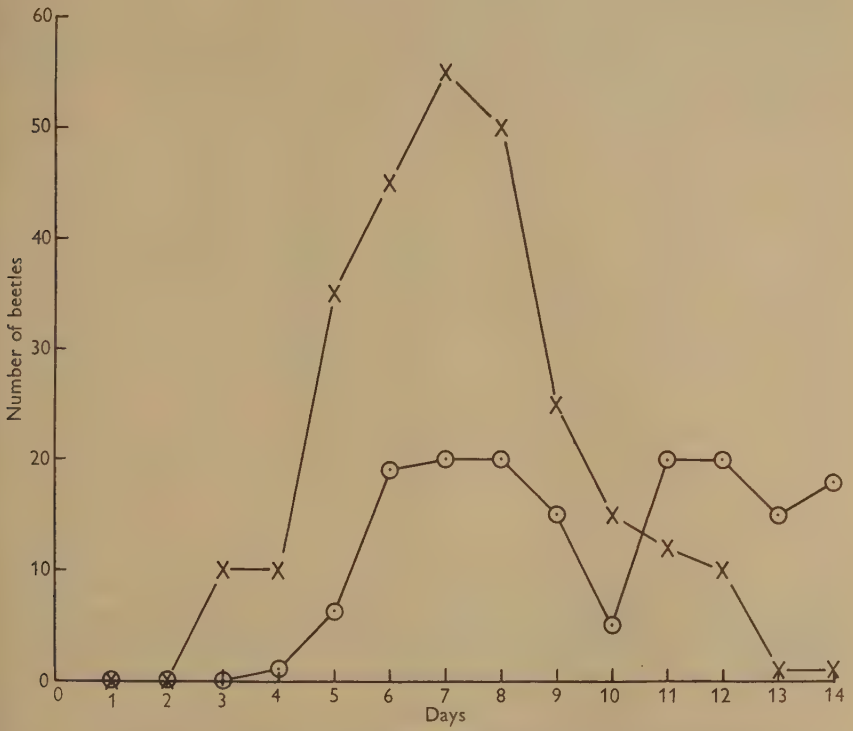

Fig. 1. Numbers of *Aleochara curtula* and *Saprinus semistriatus* visiting carcass B during the observations. ×, *Aleochara*; ⊙, *Saprinus*.

records of *N. humator* up to the end of October, but some of the specimens found during these observations were very heavily infested with mites, suggesting that they were approaching the end of their season (Fabre 1919).

The fly, *Hydrotaea armipes*, was first recorded on the 8th day. Its larvae probably lived at the expense of the blowfly larvae, and it would seem that *Hydrotaea* in Britain occupies the niche filled by *Chrysomyia* elsewhere. Both genera arrive late at the carcass and have predatory larvae with tough spiny skins.

Alysia manducator, a Braconid parasite of dipterous larvae, was first observed on day 4 at carcass B and on day 5 at carcass C. No more than five specimens were seen at any one time, and it is doubtful if the degree of infestation was high. Graham-Smith (1919) has shown that the degree of parasitism is much higher in the autumn than in

the summer. Salt (1932) regards *A. manducator* as an effective parasite since, because of the habit of ovipositing in half to full-grown larvae (Altson 1920), it attacks the dipterous larvae after the effects of overblowing have become apparent. This contrasts with the Cynipid, *Figites laevigatus*, which was first recorded on day 10. This species oviposits only in first- and second-instar larvae and shows a preference for hatchlings (James 1928) with the result that a number of larvae are parasitized which would have died in any case due to their inter-specific competition.

The whole succession may be drawn together by constructing a food chain (Fig. 2). In this the division into scavengers and predators becomes evident, and it can be seen that, apart from the dipterous larvae, no great numbers of scavengers were involved, almost all the other insects being predators or parasites of the larvae.

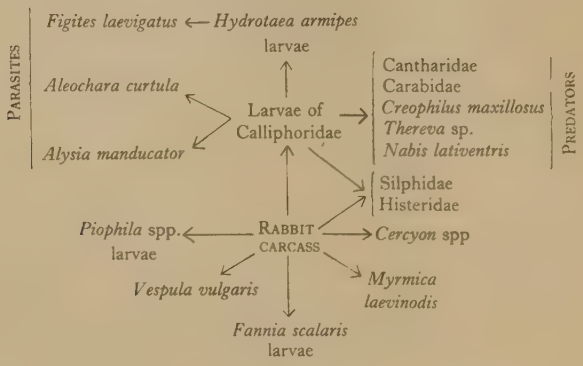

Fig. 2.

Some attempt has been made to correlate the frequency of visiting adult insects with the weather conditions (Table 2). The weather data were taken from the station in the grounds daily at 0900 h G.M.T. The rainfall figures refer to the previous 24 h.

The total number of insects increased over the first five days, this being connected with the stage of decomposition. On the 5th day Coleoptera and Hymenoptera first appeared in numbers and altogether 113 insects were counted. Days 6 and 7 were dull and the numbers of insects observed decreased, although air temperature remained high. Numbers rose sharply on the 8th day, which was warm and sunny, but fell again next day which, despite the presence of sun, was cold and very wet. On this day there was a large reduction in the numbers of beetles present, but this was probably associated with the maturation of the *Aleochara* rather than with the weather. Day 10 continued cold but less wet, with an increase in the numbers of adult Diptera. The fly larvae were not apparent from the outside on day 10, although they were seen in some numbers on subsequent days. It is probable that on day 10 they took refuge within and below the carcass to avoid the low temperatures. After this the numbers of insects observed rose again as the weather improved and temperatures went up, but the numbers recorded were never as high as those obtained previously. This was probably due to the fact that the corpses were now losing their attraction for many of the insects.

The dipterous larvae were the only scavengers of any consequence in the decomposition of the carcasses. They provided the basis on which the rest of the fauna, consisting mainly of predaceous beetles and parasitic Hymenoptera, depended. In two of the carcasses described here three stages of decomposition were observed, but in the third carcass the second stage was greatly prolonged, no drying of the corpse

Table 2. *Summary of weather conditions and adult insects visiting the carcasses during the observations*

For purposes of tabulation the weather is described as: sunny—clear sky, bright sun; cloudy—bright day, sun obscured by cloud; dull—heavy, overcast day.

Date (July)	Day	Temp. (° C)	Rainfall (mm)	Weather	Insects				
					Diptera	Hymen-optera	Cole-optera	Other orders	Total
5	1	18·5	0	Sunny	15	10	1	11	39
6	2	19·7	0·7	Sunny	14	—	2	5	21
7	3	19·1	0, heavy dew	Dull	38	5	10	—	53
8	4	19·5	0	Cloudy	31	2	22	—	55
9	5	19·8	0	Sunny	26	25	62	—	113
10	6	19·7	3·4	Dull	—	5	68	5	78
11	7	20·0	0	Dull	36	—	48	5	± 84
12	8	19·7	2·0	Sunny	33	1	84	10	138
13	9	17·7	10·0	Sunny	5	—	38	1	44
14	10	17·5	0·3	Dull	20	1	29	—	50
15	11	18·7	0	Sunny	30	20	21	21	92
16	12	19·3	0	Sunny	25	1	34	—	60
17	13	20·0	0	Sunny	20	6	36	5	67
18	14	21·0	0	Sunny	45	6	32	—	83
Total insects visiting the carcasses					339	82	487	63	

occurring before the end of the observations. The most abundant beetles were the Staphylinid *Aleochara curtula* and the Histerid *Saprinus semistriatus*. Numbers of adult insects varied from day to day with the weather conditions but showed an overall increase during the first eight days, followed by a decrease over the next six, this being correlated with the state of decomposition of the carcasses.

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SMALL MAMMAL COMMUNITIES OF THE NORTH SCANDINAVIAN BIRCH FOREST

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(With 1 Figure in the Text)

This paper presents an analysis of a collection of small mammals from a number of habitats in Troms County of north Norway. The primary purpose of the work was to obtain live specimens of *Clethrionomys* for a genetical study of species relationships in this genus, but since the animals were collected by a standardized live-trapping technique the records yield some new information on the composition of the small mammal communities of this relatively little studied region, in a form which permits comparison with collections by similar methods from other districts. The reproductive activity of the animals is the subject of a separate study by Hoyte (1955).

The collection was made in the neighbourhood of Rosta at latitude 68° 58′ N., longitude 19° 42′ E. This is a district of high relief on the western side of the main watershed of northern Scandinavia, where deeply cut U-shaped river valleys penetrate far inland and are separated by mountains rising to summits of about 1700 m. The floor of the valley at Rosta is only about 100 m above sea-level, although it lies some 80 km inland from the head of its fjord. To the east and south the general level of the ground rises progressively to the plateau of Swedish Lapland (Lappmark). There is in consequence a considerable variety of types of vegetation, arranged for the most part in sharply defined horizontal bands across the mountain sides, and providing major differences of habitat for the animal communities. Forests of birch, and in some places conifer, cover the valley floor and lower slopes of the mountains, except where areas have been cleared for farming. The cleared areas are discontinuous and rarely more than a few acres in extent. Above the upper limit of trees are various sub-alpine associations, which give way at still higher altitudes to a more sparse arctic-alpine type of vegetation.

The area studied included a part of the valley floor and the northern slope and summit plateau of Kamnasfjell, a low mountain mass to the south of Rosta. The estimated vertical range of this area was about 500 m, and its topography is represented in the profile diagram, Fig. 1, which shows the relations between the principal zones of vegetation in which trapping was carried out. These included birch forest, meadowland and several types of lower mountain associations above the tree line, but not coniferous forest or high mountain associations. The forest covered approximately the lower third of the mountain slope and was succeeded by a well-defined belt dominated by heath plants, termed here the *Empetrum nigrum* zone. The latter extended a further 100–150 m vertically up the slope before giving way to a fjaeldmark type of vegetation on the summit plateau.

The following descriptions of the vegetation of the areas trapped have been com-

piled from studies by Mr D. F. Dorward of the actual sites and more general surveys of the surrounding areas. They do not represent the exact vegetation of any given site trapped, but are rather a conspectus of the principal vegetation zones in the district. It is felt that this method gives the most useful description of the plant associations which characterize the various small mammal habitats. The nomenclature followed is that of Lid's (1952) *Norsk Flora.*

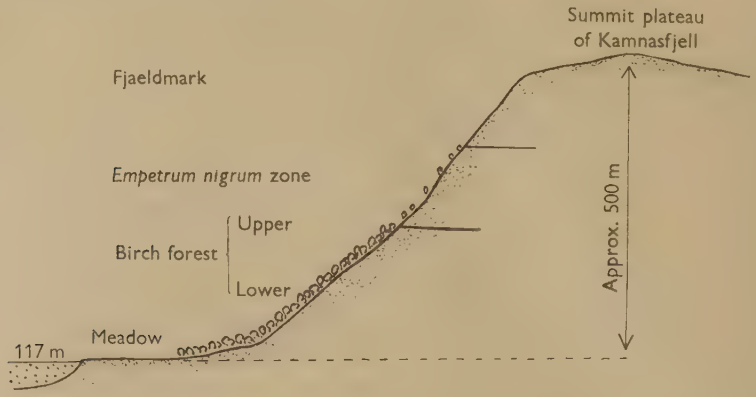

Fig. 1. Profile diagram of the area trapped to show the approximate vertical distribution of the principal vegetation zones.

(1) Fjaeldmark

Hedberg, in Hedberg, Mårtensson & Rudberg (1952), has given a detailed botanical description of the Pältsa district of northern Sweden, which lies about 20 km to the east of Rosta. The vegetation of the areas trapped on Kamnasfjell was closely similar to one or other of the low- and mid-alpine associations defined therein. Much of the summit plateau in particular was covered by various '*Dryadion*' alliances described by Hedberg. On the drier parts there was an open vegetation with patches of bare rock and soil. The most characteristic flowering plants were *Dryas octopetala, Silene acaulis, Antennaria dioica, Veronica alpina* and *V. fruticans, Loiseluria procumbens, Cassiope hypnoides* and *C. tetragona, Saxifraga oppositifolia, S. stellaris, Gentiana nivalis, Diapensia lapponica, Hieracium alpinum, Pedicularis lapponica, Bartsia alpina,* the prostrate willows *Salix herbacea* and *S. lanata,* and the grasses *Poa alpina, Phleum commutatum.* Few of these grew to more than 2 or 3 cm in height and many of them formed low cushion mats. Mosses and lichens, e.g. *Rhacomitrium, Cladonia* and *Cetraria* spp., were always to be found, particularly on the drier ground. The dwarf birch and willow, *Betula nana* and *Salix lanata,* grew only in the more sheltered places, while *Eriophorum vaginatum* and *E. angustifolium, Carex* spp., *Pinguicula alpina, Saxifraga aizoides, Andromeda polifolia, Equisetum pratense* and in places *Rubus chamaemorus* were typical of the damper situations.

(2) *Empetrum nigrum* zone.

This term is used in this paper to define a rather clearly marked zone of transition between the upper birch forest and the alpine associations. It appears to fall within Hedberg's low-alpine type of association dominated by heaths. On the north face of Kamnasfjell it occupied a belt some 100–150 m in height. Birch trees, *Betula verrucosa,* were confined to the more sheltered places. They were mostly small and scattered and did not form a canopy. The ground vegetation was dominated throughout most of the zone by the Ericaceous shrubs *Empetrum nigrum* and *Vaccinium uliginosum,* and in these areas the only other common plants were *Vaccinium myrtillus, V. vitisidaea, Phyllodoce caerulea, Arctostaphylos alpina* and *Rubus chamaemorus. Geranium sylvaticum, Trollius europaeus, Cornus suecica* and *Filipendula ulmaria*

were common but confined to strictly limited areas, usually the flatter parts of terraces, where they were often associated with grasses, small birch trees and knee-high thickets of *Salix lanata*. They formed rather distinct pockets within this zone dominated by heaths.

(3) Birch forest

This covered most of the valley floor and extended vertically about 150–200 m up the slope of Kamnasfjell. The dominant tree was *Betula verrucosa*, which formed a true canopy, except where it had been thinned or felled out. The largest specimens grew to a height of about 10 m. Other trees present were *Sorbus aucuparia* on the upper slopes; *Alnus incana* and *Salix* sp., in the wetter places near the valley floor. The ground vegetation varied from areas largely covered by the mosses and ferns, *Polytrichum commune*, *Thuidium tamariscinum*, *Dryopteris linnaeana* and *D. filix-mas*, to dense thickets of *Rubus idaeus*, and *Filipendula ulmaria*. In many places the dominant undershrub was *Vaccinium myrtillus*. Other common plants were *Geranium sylvaticum*, *Cornus suecica*, *Linnaea borealis*, *Rubus saxatilis*, *Geum rivale*, *Solidago virgaurea*, *Pyrola rotundifolia*, *Equisetum pratense* and the grasses *Deschampsia caespitosa*, *Melica nutans* and *Milium effusum*.

(4) Meadow

The cleared areas of the valley floor were for the most part under hay, though small patches of potatoes and rye were cultivated near the farms. The species of grass present were not studied. As used here the term meadow included some marshy areas where *Carex* spp., *Ranunculus repens*, *Caltha palustris* and in places *Equisetum fluviatile* and *Eriophorum angustifolium* to a large extent replaced the common meadow grasses.

Continuous trapping was carried on for 43 days, from 11 July to 23 August, with Longworth small mammal traps of the normal production type (i.e. not modified for retaining the pygmy shrew, *Sorex minutus*). One hundred traps were kept on the ground continuously except on the first and last days when only fifty were in place. They were worked in batteries of twenty-five traps and with one or two exceptions, which are detailed below, were set in a standard type of quadrat consisting of five rows of traps at intervals of 5 m. The traps were examined daily; any which contained an animal was removed and a fresh one put in its place. Whole oats were used as bait, and there was no pre-baiting of the sites.

Twenty-three sites in all were trapped. At nineteen of these the standard quadrat was set; two others were worked with twenty-five traps in groups of five placed at irregular distances from one another, and one with twenty-seven traps in three lines of nine at 5 m intervals. The remaining unit was a group of four traps placed around a farm building.

A battery of traps was moved to a new site whenever it failed to take an animal of any species for three successive days. The length of time for which different batteries remained on the ground was very variable in consequence. For instance, one quadrat was worked for 34 days and was still taking from two to four animals daily at the end of the trapping period. At the other end of the scale, nine of them took no animals during the first 3 days and were therefore moved to new sites.

ANALYSIS OF COLLECTIONS

The full trapping period yielded 218 animals belonging to the following six species:

Insectivora: *Sorex araneus* Linn., *Neomys fodiens* Schreber.

Rodentia: *Clethrionomys rutilus* Pallas, *C. rufocanus* Sundevall, *Microtus agrestis* Linn., *M. oeconomus ratticeps* Keyserling & Blasius.

The distribution of animals according to habitats is given in Table 1. Four principal habitats were recognized (meadow, birch forest, *Empetrum nigrum* zone and fjaeldmark), but it is more revealing to treat the data in six categories by dividing the forest into upper and lower sections, and separating also those quadrats which were set athwart the boundary of the meadow and forest.

Table 1. *Summary of the trapping records from different habitats*

				No. of animals						Catch rate (anima trap day
	Habitat	No. of quadrats	Total trap/days	*Clethrio-nomys rutilus*	*C. rufo-canus*	*Microtus agrestis*	*M. oeco-nomus*	*Sorex araneus*	*Neomys fodiens*	Total animals	
1.	Fjaeldmark	3	228	0	0	0	0	0	0	0	0
2.	*Empetrum nigrum* zone	5	650	3	3	0	0	13	0	19	0·029
3.	Birch forest, upper	4	675	15	0	0	0	17	1	33	0·049
4.	Birch forest, lower	7	1725	48	1	1	0	56	2	108	0·063
5.	Meadow-forest border	2	550	12	0	0	3	7	1	23	0·042
6.	Meadow	2	314	0	0	2	29	1	3	35	0·111
	Total	23	4142	78	4	3	32	94	7	218	0·053

The small mammal population was obviously not uniform in composition in all habitats. The most striking differences were found in the distribution of the voles. Except for a single specimen, all the *Microtus* of both species were taken in the meadow or along the border of the meadow and forest. *Clethrionomys rutilus* was the characteristic rodent of the birch forest, where it accounted for 45 % of the catch. It was not taken in the meadow but extended up into the lower part of the *Empetrum nigrum* zone. *Clethrionomys rufocanus*, on the other hand, appeared to favour the latter habitat. Although only four were taken in this collection, additional specimens from another locality confirmed the association of this species with the *Empetrum nigrum* zone. This point is discussed further in a later section. Of the shrews *Sorex araneus* was taken in all habitats except fjaeldmark, and in most places accounted for a considerable fraction of the total catch. *Neomys fodiens*, however, seemed to prefer the low-lying and damper parts of the forest and meadow, since six of the seven specimens were taken in quadrats on the valley floor.

(*a*) *Catch-rates and population densities*

Table 1 shows also the amount of trapping effort and the catch-rates for all animals from each habitat. The former is the sum for all sites trapped of the product of the number of traps and the length of time they were worked in days, while the latter is defined as the number of animals caught divided by this figure. The catch-rate provides a simple basis for comparing the relative population densities of habitats to which different trapping efforts were devoted.

There is a clear tendency for the catch-rate to fall, irrespective of the species composition as we proceed from the valley floor to the summit plateau. The rate of decline is remarkably regular considering the relatively small numbers of animals on which the

catch-rates are based, and probably reflects a similar fall in the population densities. The effect is apparent even within the limits of the birch forest if the results from sites on or close to the valley floor are compared with those higher up. Only the quadrats which were set across the meadow-forest boundary gave a catch-rate lower than might be expected on the view that there was a positive correlation between the population density and altitude. It may well be, however, that the boundary zone between these two major habitats is not particularly favoured by the inhabitants of either.

The fact that no animals were taken on the fjaeldmark does not mean there were none there, but that their density was so low that the chance of making a catch in any given quadrat was small. *Lemmus lemmus* was seen in the area, and the traps were set around sites where there were fresh droppings of some species of Microtinae. It is possible, however, that lemming, being a larger animal than the other species taken, will not readily enter a Longworth trap.

(*b*) *Changes in the population during the trapping period*

The weekly catches of *Clethrionomys rutilus*, *Sorex araneus* and the total for all species are presented in Table 2. It shows that most animals were taken during the second half of the trapping period, corresponding roughly with the first 3 weeks of

Table 2. *The weekly catch of* Clethrionomys rutilus, Sorex araneus *and all species*

Each week consisted of approximately 700 trap/days, except the first and last, which were of about 650 trap/days each.

	C. rutilus		*S. araneus*		
	No.	% of total catch	No.	% of total catch	Total, all species
1. 11–18 July	1	—	0	—	1
2. 19–25 July	15	60	7	28	25
3. 26 July–1 Aug.	15	43	10	28	35
4. 2–8 Aug.	18	33	19	36	54
5. 9–15 Aug.	18	37	24	50	48
6. 16–22 Aug.	11	21	33	62	53
Totals	78		93*		216*

* Note. The final day's trapping is not included. One specimen of *Sorex araneus* and one of *Microtus oeconomus* were taken from four traps remaining on the ground till 23 Aug., bringing the total of all species to 218.

August, during which time the total catch remained nearly constant at about fifty animals a week. By contrast, the total catch during the first 9 days from 11 to 20 July was a single specimen of *Clethrionomys rutilus*. No simple explanation can be offered for this large difference in the success of the two halves of the trapping period. It appears to be due partly to the discovery of productive areas by trial and error, and partly to a real increase in the population of certain species as the summer progressed. During the first week the sites trapped were distributed from the valley floor to the summit plateau. All of them were equally unproductive, though several quadrats in similar situations nearby gave good catches later on in August.

The trend of the weekly catches of *Clethrionomys rutilus* and *Sorex araneus* is of some interest. Omitting the first week, the catch of *Clethrionomys rutilus* was fairly constant, averaging about two a day. The numbers of *Sorex araneus*, however, rose steadily, accounting for an ever increasing fraction of the total catch from about a quarter in the second week to nearly two-thirds in the last. At first sight these figures suggest that the population density of the vole in the birch forest was more or less constant, while that of the shrew increased some two- or threefold during the 6-week period. In the case of *Sorex*, Hoyte's study of the reproductive condition of the specimens supports this view. A large fraction of the shrew catch in July consisted of pregnant females carrying seven or eight foetuses, and males and females were taken in approximately equal numbers. In August twice as many males were taken as females, and few of either sex had yet bred. The gestation period of the species is from 13 to 19 days, and according to Brambell (1935) it breeds from May to September in Britain. It is probable that the breeding season in northern Scandinavia does not begin before the middle of June, and is at its height in July. It is to be expected therefore that by August the population density will be increasing rapidly with the appearance of animals which are the product of the same season's breeding activity.

The situation as regards *Clethrionomys rutilus* is not so clear. There was no striking overall increase in the proportion of young animals in the later part of the trapping period, though some increase was observed in the proportion of females which had not yet bred, and the sex ratio remained constant at about two males caught to every female.

(*c*) *Comparison with other populations*

It is of interest to compare the small mammals of Rosta with other populations, in particular with the collections made in 1951 by similar methods from five localities in the Bergen and Hardanger districts of southern Norway and described by Steven (1952). Seven species were found in southern Norway compared with six at Rosta, but not more than five were taken at any one locality. Five species were common to both collections, namely the two shrews, both species of *Microtus* and *Clethrionomys rufocanus*. The two southern species not found at Rosta were *Apodemus sylvaticus* and *Clethrionomys glareolus*, while *C. rutilus* was only taken from there. According to Collett (1911–12), the northern limit of the distribution of *Apodemus sylvaticus* is at about 62° N., of *Clethrionomys glareolus* at 67° N. in Saltenfjord, while *C. rutilus* is said to reach its southern limit close to Rosta in the Maals river valley.

There are in Norway three clearly differentiated species of *Clethrionomys*. Two of them, *C. glareolus* and *C. rutilus*, appear to form a replacement pair with non-overlapping geographical distributions. Allowing for some uncertainty in our knowledge of the exact limits of their ranges, it seems unlikely that they can be in contact with one another except in a narrow zone between 67° and 69° N. There is, moreover, some evidence that in the birch forest they may be direct competitors in the demands they make upon the resources of the environment. Most of the specimens of *C. glareolus* collected by Steven (1952) from several localities in western Norway were taken in upland birch forest and birch scrub close to the upper limit of trees, and few were taken from any other habitat. Although the species occurs throughout most of

northern and central Europe in a great variety of habitats, it appears towards this northern periphery of its range to be more or less restricted to the birch forest, in which presumably it finds its optimum niche. If this is true, its northward distribution is probably limited by competition with *C. rutilus* rather than by environmental factors. A study of the ecology of the two species in the region between 67° and 69° N. would be of great interest and should provide the information needed to settle this point.

C. rufocanus, on the other hand, has been taken at several places from the same trap lines or quadrats with another species of *Clethrionomys*. At Rosta it was found with *C. rutilus*, at Finse and Mjølfjell in west Norway with *C. glareolus*. Though formerly regarded as a northern species, it is from Hagen's (1950) studies of the pellets of birds of prey now known to be widely distributed in the mountains of southern Norway. We cannot, however, discover much about its ecology in this way. In my experience it shows a marked preference for dry rocky situations dominated by heath vegetation close to or above the upper limit of trees. At Rosta it was associated with the *Empetrum nigrum* zone, and at Mjølfjell in 1951 it was common in a similar habitat, a steep slope of old scree partly overgrown with *E. nigrum* and small birch trees at an altitude of about 800 m. Another small collection of ten specimens, not otherwise included in this study, was obtained in 1953 from Lyngsdal on the Lyngen Peninsula at 60° 30′ N. from a habitat which also closely resembled the *E. nigrum* zone at Rosta. Finally, at Finse in 1951 the situation was dry and boulder strewn, although in the true arctic-alpine zone above the limit of trees.

Although precise knowledge of its habits is still lacking, these findings suggest that *Clethrionomys rufocanus* differs from the other two species in some aspects of its ecology. It appears to be more restricted in its choice of country but within its preferred habitat can hold its own and co-exist with either *C. glareolus* or *C. rutilus*.

The case of the two species of *Microtus* differs from that of *Clethrionomys* in certain respects. The two species are very much alike, the more intermediate and some of the immature specimens especially being almost impossible to distinguish taxonomically when alive. In this work certain specimens were only identified with certainty after death by detailed examinations of their teeth and body measurements. In 1951 *Microtus oeconomus ratticeps* was taken only at Finse at an elevation of about 1300 m in the arctic-alpine zone. Since according to Collett it is confined in southern Norway to the high mountains, there seemed to be some ground for thinking that it replaced *M. agrestis* at high altitudes. Wildhagen (1953) states, however, that it is found in the arctic and sub-arctic zones throughout the greater part of the country, while *M. agrestis* occurs all over the country from the coast to the mountain plateaus. At Rosta *M. oeconomus ratticeps* was the common vole of the meadowland on the valley floor and was not found in any other habitat. Two of the three specimens of *M. agrestis* were taken in the same habitat and the remaining one in the birch forest nearby. There is no question here of the two species forming a replacement pair in respect of altitude, nor was there any apparent difference in their choice of habitat. Elton (1942) has stated that *M. oeconomus ratticeps* often inhabits the low willow scrub by streams and tarns, but this was not found to be generally true at either Finse or Rosta. We must accept for the present that no difference has been demonstrated in the ecology of these

two species in those areas where they occur together, though there may be a shift in the balance of advantage between them in the north compared with southern Scandinavia.

(*d*) *Comparison of catch-rates*

Table 3 shows the catch-rates for the full period and for the first 24 h trapping from the different habitats at Rosta and for the five localities in southern Norway studied in 1951. Comparison of these rates supports the view expressed by Steven (1952) that the catch during the first 24 h gives a good indication of the yield that a longer spell of trapping is likely to produce. As in 1951, the correspondence between the shorter and longer periods was in most cases remarkably close, particularly in the birch forest where the trapping effort was greatest. The only large divergence was in the *Empetrum nigrum* zone, which gave a much better catch-rate over the longer period.

Table 3. *Comparison of catch-rates for the first 24 h and longer periods from different localities and habitats*

The values from five localities in southern Norway are from Steven (1952).

	Animals/trap/day	
	First 24 h	Full period
South Norway, 1951		
Espegrend	0·28	0·24
Mjølfjell	0·16	0·12
Paradis	0·09	0·09
Finse	0·09	0·07
Svartevann	0·02	0·02
North Norway, 1953		
Rosta, fjaeldmark	0	0
Rosta, *Empetrum nigrum* zone	0·008	0·029
Rosta, birch forest (upper)	0·050	0·049
Rosta, birch forest (lower)	0·068	0·063
Rosta, meadow-forest border	0·040	0·042
Rosta, meadow	0·17	0·11

Although it is of no particular significance, owing to the well-known fact that small mammal populations fluctuate greatly from year to year and from season to season, catch-rates at Rosta were in general lower than in southern Norway in 1951 or in collections by similar methods in Great Britain (unpublished data).

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SUMMARY

A collection of 218 small mammals belonging to six species is analysed in terms of their distribution among a number of habitats.

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OBSERVATIONS ON REPRODUCTION IN SOME SMALL MAMMALS OF ARCTIC NORWAY

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There is relatively little information on the reproductive activity of small mammals in arctic latitudes. This study was made in order to collect information, and to compare it with that derived from more southerly populations.

Material was collected in Norway at Rosta (68° 58′ N., 19° 42′ E.) between 11 July and 23 August 1953. The primary object of the trapping was to obtain some live specimens of *Clethrionomys* and a few of *Microtus oeconomus*, but many specimens of other small mammals were caught at the same time. Information on the ecology of these animals is contained in the paper by Steven (1955). The full trapping period

Table 1. *Material—numbers of animals*

	Trapped		Examined	
	Males	Females	Males	Females
Sorex araneus Linn.	60	34	60	34
Neomys fodiens Schreb.	4	3	4	3
Clethrionomys rutilus Pallas	50	28	26	15
C. rufocanus Sundevall	2	2	1	1
Microtus agrestis Linn.	1	2	1	2
M. oeconomus ratticeps Keyserling & Blasius	11	21	8	17

yielded 218 animals. All except those wanted alive were measured and were available for later examination. Table 1 shows the species that were taken in the traps, the numbers of males and females trapped, and the numbers examined.

METHODS

The trapping methods which were used are outlined by Steven (1955). Some of the *Sorex araneus* died in the traps, otherwise most specimens were killed immediately before examination. They were weighed on a spring-balance accurate to the nearest 0·5 g, and the total length and the head-and-body length were measured to the nearest millimetre. The body weight and the length of head-and-body are used as criteria of size in this paper. The specimens were dissected and the state of their sex organs noted. All material was preserved in Bouin's fixative and brought back to this country for microscopical examination. Serial sections, each of 15μ thickness, were made of the male organs and some selected for staining and examination. Similar sections were made of the female primary sex organs and every fifth section selected. The sections were stained with Heidenhain's iron haematoxylin and counterstained with eosin.

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RESULTS

(*a*) Sorex araneus *Linn.*

Sixty males, caught between 21 July and 22 August, were examined and six of these were found to be sexually mature. These weighed 8, 8·5 or 9 g, had a head-and-body length of from 70 to 80 mm, and testes which were distinctly larger than those of immature animals. The immature males ranged in body weight from 3 to 6·5 g, and in head-and-body length from 58 to 71 mm. No males weighing 7 or 7·5 g were caught. No sex organs were weighed, but it is probable that the much larger testes and accessory sex organs of the mature animals accounted for their distinctly greater body weight. No testes intermediate in size between those of adult and of juvenile animals were found, which indicates that no young male approaches puberty at this time of year. By the end of the first week in August, sixteen of the sixty specimens had been caught, in the proportion of one adult to seven juveniles. This changed to 1:10 during the remaining period of trapping when forty-four specimens were caught, indicating that the proportion of juveniles in the population rose as the breeding season advanced.

Thirty-four females, caught between 19 July and 23 August, were examined and six were found to be sexually mature; these all weighed 8 g or more. The primary sex organs were appreciably larger than those of immature animals. The head-and-body length gave no guide to maturity; both the longest (80 mm) and the shortest (64 mm) animals of the series were mature. The other mature animals ranged in length from 67 to 71 mm, and the immature ones from 65 to 71 mm. The body weights of immature animals ranged from 4·5 to 7 g. No animals weighing 7·5 g were caught; as in the males, this was probably associated with the much greater size of the sex organs in the mature animals.

Four of the six mature females were pregnant, with implanted embryos numbering 8, 8, 8 and 7. None of these four was observed to be lactating; their sex organs were not examined microscopically so that it is not known if they were parous or non-parous. The fifth was lactating; the ovaries contained a total of 11 (9+2) corpora lutea, and unimplanted early blastocysts were found in the uterus. Only three were found, but it is probable that others were lost in discarded sections. The sixth mature female was lactating also, but the ovaries were small, inactive and lacked any large follicles.

The trapping yielded twice as many males as females, but the absolute number of mature animals of each sex was the same. The mature males were caught throughout the period of trapping, but the mature females were all caught at the beginning of the period. Indeed, by the evening of 24 July, five of these females had been taken but only one male. The sixth and last mature female was caught on 3 August. During the rest of the month they may have been avoiding the traps, but it is more probable that there was, in fact, a great reduction in the number of mature females in the area at about this time.

(*b*) Neomys fodiens *Schreb.*

Four males, caught between 30 July and 5 August, were examined, but none was sexually mature. Their body weights were 9·5, 9, 8 and 8 g; their head-and-body lengths were 76, 71, 77 and 72 mm, respectively.

Three females were caught; one each on 9, 11 and 12 August. One was sexually mature; it weighed 16 g and had a head-and-body length of 90 mm. The two immature females weighed 11 and 8·5 g, and their head-and-body lengths were 75 and 82 mm respectively.

The mature female had ovaries which were dark red and nearly spherical, with a greatest diameter of 5 mm, compared to 1·2 mm in the immature females. Each ovary was composed largely of corpora lutea which were closely packed together into a single rounded mass. The corpora could not be distinguished from each other and counted because there were no apparent boundaries between them, except near the surface of the ovary where small follicles occurred. Thirteen unimplanted blastocysts were counted in the uterus.

(*c*) Clethrionomys rutilus *Pallas*

Twenty-six males, caught between 17 July and 20 August, were examined and eleven were found to be sexually active. Material from sixteen additional specimens was discarded in the mistaken belief that it was possible to deduce, as in *Sorex araneus*, whether a specimen was sexually active or inactive from its size and from the size of its testes.

Examination of sections of the testes and epididymes of sexually inactive animals showed that they fell into three groups. All had comparatively small testes. Group 1 consisted of those with division figures in the germinal epithelium but no spermatozoa; the lumen of the epididymal tube was narrow and wholly or partly choked with debris, apparently thrown off by the cells lining the lumen. Group 2 consisted of those again lacking spermatozoa and with division figures in the germinal epithelium, but the lumen of the epididymal tube was as wide as in sexually active males and was nearly free of debris. Group 3 consisted of those lacking spermatozoa but with very few or no division figures in the germinal epithelium. The lumen of the epididymal tube was again wide and nearly free of debris. The nuclei of the germinal epithelium in group 3 testes took up comparatively little stain. They stood out from the wall in some tubules and were arranged in a ring. This condition is reminiscent of that described by Rowlands (1936) as the winter aspermatogenesis in the English bank vole, *Clethrionomy* (*Evotomys*) *glareolus*.

Group 1 animals ranged in body weight from 7 to 13 g and head-and-body length from 73 to 83 mm. Corresponding measurements for groups 2 and 3 animals together were 10–16 g and 82–98 mm, and for sexually active animals were 10–20 g and 79–102 mm. The first known group 2 animal appeared in the traps on 7 August; the first group 3 animal on 11 August; no sexually active animal was caught after 15 August. Group 1 animals appear to be the juvenile males, and they were in general smaller than the sexually active males. The evidence from the microscopic examination of the testes and epididymes, from the measurements and from the dates of capture of animals of groups 2 and 3 suggests that they were animals that had been sexually active earlier in the season, and that the end of the breeding season occurred in the middle of August in this region.

Before the end of the first week in August, the male population consisted of sexually active animals and of juveniles. It is not possible to establish with certainty that the

juveniles born early in the season reached maturity before its end, but judging by the continuity of measurements, this does seem probable. There was no apparent increase in the proportion of juveniles in the population as the breeding season advanced. The exact proportion is in any case uncertain because some specimens were not fully examined, but estimates of the ages of these suggest that the proportion of adults to juveniles caught during July was 10:4, and during August was 19:9. This was a surprisingly low proportion of juveniles. If some juveniles did reach maturity before the end of the season, it would provide a partial explanation for their continued low proportion.

Fifteen females, caught between 24 July and 22 August, were examined; ten were found to be sexually mature, five were immature. The five immature animals had head-and-body lengths of 74–85 mm, and body weights of 7–11 g. The majority of the ten mature animals had head-and-body lengths of 88–110 mm, but two measured only 79 and 81 mm. The mature animals had body weights from 12 to 34 g, inclusive of embryos, but one weighed only 8·5 g. Two other animals, which were not fully examined, measured 77 and 95 mm, and weighed 12 and 15 g respectively. The former was therefore probably immature, the latter mature. The ten sexually mature animals were made up of seven which were fully pregnant, one which had unimplanted blastocysts throughout the uterus, one which had unimplanted blastocysts still in the uterine end of the fallopian tubes, and one which had a seminal plug in the vagina; spermatozoa had penetrated far up the fallopian tubes, where some of the ova had just been fertilized. Thus all ten of the sexually mature animals which were examined were effectively pregnant. An eleventh animal, which was one of the two not fully examined but was probably mature, showed no gross signs of pregnancy, but it may have been in an early stage. The incidence of pregnancy at this time of year was therefore at least 91 %. This figure is probably too high, for the reason adduced on p. 416.

The embryos in six of the seven fully pregnant animals numbered 10, 10, 9, 8, 7 and 6. The seventh animal was pregnant when caught and survived to bear and rear a litter of young, which unfortunately were lost on the voyage back to England. The young were first counted when the litter was three or four days old; only five were found. However, examination of sections of the mother's uterus showed nine implantation sites. Twelve similar implantation sites were found in the female which had unimplanted blastocysts in the uterus. The average number of embryos is therefore 8·9 if implantation sites are included also. The average litter size is probably smaller than this because if the implantation sites, which must have included those where embryos were reabsorbed, are excluded from the count, the average number of embryos is only 8·3.

Table 2 shows the number of embryos in relation to the number of corpora lutea in each pregnant female. There does not seem to be any relation between number of embryos and degree of success of fertilization and implantation. The average number of ova shed per ovulation is 9·2. In one of these pregnant animals, there were two older sets of corpora lutea. The most recent set numbered 4 in one ovary and 4 in the other; the next most recent set numbered 5 + 4; and the oldest 4 + 4. This animal had become pregnant only after it had passed through two sterile oestrous cycles. Multiple sets of corpora were also found in two other animals. One of them had recently

copulated and had sets numbering 5 + 4, 5 + 6, 7 + 5, in order of increasing age. The other animal had unimplanted blastocysts in the uterine end of the fallopian tubes and no implantation sites in the uterus; the sets here numbered 3 + 6, 5 + 5, 4 + 5. The average number, derived from all animals examined, of ova released per ovulation is therefore 9·5. This is a little higher than the 9·2 derived from those in Table 2, which all resulted in fertilization and implantation, but the difference is not significant. The average percentage success of fertilization and implantation, using the lower of these figures and the higher of the two derived for the average number of embryos, is therefore 97 %.

Table 2. Clethrionomys rutilus: *pregnant females*

Number of embryos	Number of corpora lutea	Percentage fertilization and implantation
10 (8+2)	8+2	100
10 (7+3)	7+3	100
9 (5+4)	Not examined	—
8 (5+3)	8+3	73
7 (5+2)	5+2	100
6 (3+3)	4+4*	75

* Older sets also present.

The mammary glands were active in only two of the animals at the time of capture. There were ten large embryos in the uterus of one, and examination showed traces of old implantation sites. These could not be counted with certainty. The other lactating animal had unimplanted blastocysts in the uterus, and twelve old implantation sites.

The females of this series which had head-and-body lengths of 90 mm or more were all mature, all pregnant, all with only one set of corpora lutea in the ovaries; and some were lactating. (The two animals which were not fully examined are excluded from this analysis.) All those measuring less than 90 mm were either immature, or were mature and pregnant but with three sets of corpora lutea in the ovaries. This suggests that the larger females became pregnant at a post-partum oestrus if they were lactating, or at a post-lactation oestrus if they were not. This also suggests that the smaller mature females were recently immature, and that having reached maturity in the course of the breeding season they had passed through three oestrous cycles to become pregnant on the third.

The ratio of lactating to non-lactating mature females suggests that the figure of 91 %, given on p. 415, for the incidence of pregnancy, is too high. The females of the older group which were pregnant but non-lactating at the time of capture presumably passed through a non-pregnant period while lactating. Similarly, the younger females passed through a period of sterile oestrous cycles immediately after reaching maturity. The thirteen unexamined females may have included specimens in either condition.

No female with unimplanted blastocysts was caught after the end of the first week in August. It is probable that the end of the breeding season was approaching, although it would be several weeks before the last litter was weaned. This approximate date for closure of the season is confirmed by the fact that no sexually active males were caught after 15 August.

(*d*) Clethrionomys rufocanus *Sundevall*

A male, caught on 4 August, was examined and found to be sexually mature. It weighed 26 g, and the head-and-body measured 101 mm.

A female, caught on 15 August, was found to be sexually mature; it weighed only 11 g and measured 93 mm. The uterus of this female was pinker in colour than those of any *C. rutilus* which were examined, and there was a seminal plug in the vagina. Examination of stained sections showed masses of sperm in the uterus, but none in the fallopian tubes. There were two sets of corpora lutea in the ovaries. The younger set numbered only 1+2; the older, 1+1. The antra of the former were not yet obliterated and unfertilized ova were found in the ovarian parts of the fallopian tubes. This animal was not lactating and, in any case, was small. It is therefore probable that it had just reached maturity. It had passed through one sterile oestrous cycle before copulation. The occurrence of sterile cycles was noted as being typical of young *C. rutilus* which had evidently just reached maturity (see p. 416).

(*e*) Microtus agrestis *Linn.*

One male was caught on 5 August. It weighed 29 g; the head-and-body measured 107 mm. It was mature.

Two females were caught, on 7 and 16 August. Their weights were 12 and 35 g; head-and-body lengths were 87 and 109 mm respectively. The smaller animal was immature; the larger was mature and pregnant with seven embryos, but was not lactating. The ovaries of this one mature female contained seven (4+3) corpora lutea; fertilization and implantation was 100%.

(*f*) Microtus oeconomus ratticeps *Keyserling & Blasius*

Eight males, caught between 31 July and 22 August, were examined and four were found to be sexually active. These had body weights ranging from 32·5 to 49 g and head-and-body lengths from 102 to 129 mm. Of the four animals whose testes contained no spermatozoa, one weighed 48 g and measured 118 mm, but the other three were smaller, weighing from 13 to 18 g and measuring 80–90 mm. The testes of this large male were as small as those of the other three non-active males, but division figures in the germinal epithelium were fewer and the epididymal tubes, though small, were less choked. This male had therefore probably been sexually active earlier in the season; it was caught on 22 August. Its classification is confirmed by the condition of the sex organs of one caught two days previously. The production of spermatozoa appeared to be falling off in this animal, although they were still plentiful. The end of the breeding season was therefore approaching at the end of August.

Seventeen females, caught between 20 July and 22 August, were examined. All but three of these were sexually mature. The mature animals had body weights from 14 to 80 g, inclusive of embryos, and head-and-body lengths from 86 to 136 mm. The three immature animals weighed 25, 21 and 18 g and measured 92, 90 and 83 mm respectively. Examination of serial sections of the ovaries of these three immature animals revealed a number of apparently ripe follicles.

It is not possible to derive figures on the incidence of pregnancy among the mature females of this series, since five were kept alive for several weeks and used for a study on the oestrous cycle (described on pp. 420–2) and at least one of these may have been pregnant at the time of capture. Another three, which were dissected, showed no gross signs of pregnancy and were not further examined. Dissection showed that six of the other nine mature females were fully pregnant at the time of capture. The embryos in each numbered 10, 8, 8, 8, 6 and 5, an average of 7·5. Of the remaining three, one had 4-celled blastocysts still in the uterine end of the fallopian tubes, and two had shed ova, which were situated in the middle parts of the fallopian tubes in both cases, but had not copulated.

Only three animals were found to have active mammary glands. (Again, this figure may be too low because the animals which were kept alive were not examined at the time of capture.) These lactating animals were caught on 3, 7 and 8 August. One of these was fully examined, and traces of the old implantation sites could be distinguished. This lactating female had three sets of corpora lutea in the ovaries. The precise number of corpora in each of the two older sets was not easy to determine because there seemed to be no clear distinction between these sets in size and depth within the ovary, and no difference in staining properties. The corpora of the two older sets were small and took up little eosin. Nuclei were small; and cells were small and tightly packed. The youngest corpora were clearly larger and well stained. Nuclei were larger; and the cells larger, rounder and more loosely packed. The youngest set corresponded to the 4-celled blastocysts in the fallopian tubes. The numbers of corpora lutea in each set was estimated to be: 2+7, 7+2, 5+6, in order of increasing age. The two females with unfertilized ova each had only one set of corpora lutea in their ovaries. They numbered 5+1; and 4+2.

Table 3 lists the pregnant females and number of embryos in relation to number of active corpora lutea. There does not seem to be any relation between number of embryos and degree of success of fertilization and implantation. Three of these females

Table 3. Microtus oeconomus: *pregnant females*

Number of embryos	Number of corpora lutea	Percentage fertilization and implantation
10 (7+3)	7+3*	100
8 (4+4)	4+4*	100
8 (5+3)	5+3	100
8 (5+3)	6+3*	89
6 (3+3)	5+1	100
5 (3+2)	7+2	56

* Older sets also present.

had additional older sets of corpora lutea. The corpora in each numbered: 7+3, 3+6; 4+4, 7+1; 6+3, 4+4, 4+4. Two had become pregnant after the ovaries had gone through one sterile oestrous cycle; the third animal had gone through two such cycles. The average number, derived from all females examined, of ova released per ovulation is therefore 8·3. The average number derived from Table 3 of ova released per ovu-

lation resulting in pregnancy is the same. The average number of embryos is 7·5 (see p. 418). Fertilization and implantation was on the average 90% successful.

The four largest pregnant females all had ovaries which contained more than one set of corpora lutea. The three smallest all had ovaries which contained only one set. These seven animals, together with the two which contained unfertilized ova, are listed in Table 4. There is no marked gap between the range of size in the group of larger females and the range of the smaller. Slight differences in the fur coloration support such a division of these mature females into two groups. The fur of animals of this species is made up of hairs which are dark grey; those of the back are tipped with

Table 4. Microtus oeconomus: *mature females*

Head-and-body length (mm)	Sets of corpora lutea	Pregnant	Lactating
136	3	+	+
135	2	+	–
131	3	+	–
117	2	+	–
114	1	+	–
109	1	+	–
99	1	+	–
90	1	–	–
86	1	–	–

brown; those of the underside with grey. The fur along the spines of the larger females was a darker brown and richer in colour than that of the smaller females. This dark streak was noticed by Miller (1912) in one skin that he examined, but he did not attach any special significance to it. On the underside the smaller females were a clear grey in colour: the dark hairs were tipped with very pale grey. On the larger females this very pale grey was tinged with pale brown so that it seemed the fur was singed.

Examination of the sex organs in all females showed that the immature ones which were caught were about to attain maturity, and the two smallest of the mature females had just attained maturity and ovulated once. The other small mature females were primiparous; the first ovulation here was accompanied by copulation and fertilization. The older females were all pregnant, and had probably borne litters earlier in the season. Each had become pregnant again only after one or two sterile ovulations, which in at least one female began while still lactating, probably soon after parturition; in the others, ovulation may not have occurred until the previous litter had been weaned.

The sex organs showed no definite signs of an approaching end to the breeding season; no female was found with ovaries in anoestrus. The female carrying unimplanted blastocysts was caught on 7 August; no female in such an early stage of pregnancy was caught after this date, but the female carrying six embryos was caught on 20 August. However, the condition of the testes in a male caught on 22 August suggests that the breeding season was drawing to a close at about this date.

THE OESTROUS CYCLE IN *MICROTUS OECONOMUS*

Seven freshly caught specimens of *M. oeconomus* were used. They were kept in individual galvanized iron cages measuring approximately $8 \times 5 \times 7$ in., with one end of wire mesh and a lid of wire mesh or perforated zinc; except for one animal which was kept in a large biscuit tin with a perforated lid, and the two smallest animals of the group which were caged together. The cages were kept in the unheated attic of a wooden cottage. Some dry grass was given for bedding; the animals were fed potato, mixed grain (wheat and oats), and given fresh grass daily.

Starting two to four days after capture, a vaginal smear was made from each animal in the morning, and again in the evening. The vaginal smears were obtained with the blunt end of a stout darning-needle set in a cork. Each smear was stained with Leishmann's stain and later examined. Estimates were made of the relative and absolute numbers of the different cell types in each smear. The number of each was noted as +, ++, +++, in order of increasing abundance.

The smears consisted of three types of cells: leucocytes, nucleated epithelial cells and non-nucleated epithelial cells. The relative and absolute numbers of these cells passed through a cycle of increase and decrease in most respects similar to that found in mature laboratory rats and mice. It was sometimes difficult to interpret the smears, partly because of the irregularity of the changes, and partly because of persistence of the leucocytes, even in full oestrus. This is in contrast to the oestrous smear of laboratory rats and mice from which leucocytes are typically absent. These points are illustrated in Table 5 which is the record of one of the females.

In this animal there appeared first of all a normal cycle in all its stages. This was followed by a proestrus which was not succeeded by a full oestrus and then metoestrus, but by a short period of what appeared to be dioestrus. It seems improbable that these two missing stages were passed through so quickly that they escaped the twice-daily inspection. It seems probable that this was an instance of what recurred at a later date in this female and what evidently also occurred in other females in this group. There were occasions when the vagina did not reach a condition of full oestrus after a typical proestrus.

Following this period of dioestrus, there were two complete cycles which were separated by one more proestrus and anticlimax. This second anticlimax was slightly different from the first in that it initially looked to be more typical of metoestrus, but the two succeeding smears were typical of dioestrus. In this female the full cycle alternated with the proestrus and anticlimax.

A similar alternation was found in one other female, but two others apparently passed from oestrus to oestrus without intervention of proestrus and anticlimax. A fifth female yielded a series of smears which were difficult to interpret. During the first ten days, this female appeared to vacillate between dioestrus and metoestrus. Possibly this female was pregnant when trapped and during this period the embryos underwent reabsorption due to the handling and disturbance of the mother. This was followed by five successive periods of proestrus and anticlimax, and a final oestrous cycle. The two smallest females were kept alive for only nine days because, although the vaginal orifice was open in each, the smears showed them to be immature. The

ovaries were later sectioned and examination confirmed their immaturity, but maturity seemed imminent.

The duration of each stage of the cycle and of the complete cycle, measured from the beginning of one oestrus to the beginning of the next, varied greatly in different

Table 5. *The oestrous cycle in* Microtus oeconomus

Vaginal smears: record of one of the females.

	Time	Leucocytes	Nucleated cells	Non-nucleated cells	Interpretation
29 July	1815	++	++	+	Dioestrus
30	1730	+++	++	+	.
31	1600	++	++	+	.
1 Aug.	1730	+	++	+	Proestrus
2	1640	+	++	+	.
3	0930	++	++	+	.
3	1820	+	+++	+	.
4	0915	+	+	++	Oestrus
4	1755	++	+	++	Metoestrus
5	0900	++	++	++	.
5	1835	+	+	+	.
6	0810	+	++	++	.
6	1725	+++	++	++	.
7	0905	+++	++	++	.
7	1805	+++	+++	+	Dioestrus
8	0845	++	++	+	.
8	1810	++	++	+	.
9	0900	+++	++	+	.
9	1750	+++	+++	+	Proestrus
10	0900	++	++	+	.
10	1805	+	++	+	.
11	0910	++	++	+	.
11	2000	+++	++	+	Dioestrus
12	0820	+++	++	+	.
12	1820	+++	++	+	.
13	0825	+++	++	+	.
13	1800	++	++	+	.
14	0810	+	+++	+	Proestrus
14	1755	+	+++	+	.
15	0900	+	+++	++	.
15	1810	++	++	+++	Oestrus
16	0850	++	+	++	Metoestrus
16	1820	+	++	++	.
17	0820	++	+	++	.
17	1805	++	++	++	.
18	0855	++	+++	++	Proestrus
18	1835	+	+++	+	.
19	0840	++	++	++	Metoestrus
19	1760	+++	+++	+	Dioestrus
20	0950	++	++	+	.
20	1910	++	+++	+	Proestrus
21	0910	+	+	++	Oestrus
21	1945	++	++	++	Metoestrus
22	0915	+	+	++	.

females and in the same female at different times. Each of the stages, at one time or another, evidently lasted for less than one day. The maximum length of time for which each stage persisted was as follows: proestrus, three days; oestrus, four days; metoestrus, five days; dioestrus, seven days. The average duration of the complete

cycle, based on a total of six instances, was about eight and a half days, varying from six to eleven days.

These observations show that *Microtus oeconomus* is polyoestrous. This is corroborated by the evidence from the other specimens, whose sex organs were stained and examined. These observations also suggest that this species ovulates spontaneously. This too is corroborated by the findings on other specimens (see pp. 418 and 423).

The occurrence in some of these females of proestrus smears which were not followed by oestrus may be due to the disturbances of captivity and twice-daily handling. However, it is suggestive that Dewar (1945) found this condition in the Norway rat, *Rattus norvegicus*, examined in October when fertility was falling off to the winter level. The occurrence of this proestrus and anticlimax in these female *Microtus oeconomus* possibly indicated an approaching end to the breeding season. This suggestion is corroborated by the finding of a male in which spermatogenesis had ceased (see p. 417), but the evidence from the females themselves was not so positive (see p. 419).

DISCUSSION

This collection of small mammals of arctic Norway was started in July. Examination of sex organs showed that the breeding season was then well advanced for all species. Enough material was collected in August to show that the shrew, *Sorex araneus*, stopped breeding in the early part of the month; the vole, *Clethrionomys rutilus*, in the second week; and the vole, *Microtus oeconomus*, in the latter part of the month. These dates are all earlier than those found by authors whose material was collected in more southern latitudes. Brambell (1935) found that *Sorex araneus* stops breeding in September or October in England and Wales. He concluded that the end of the breeding season is probably determined by the females, since males with sperms were obtained after the last pregnant female in the autumn. The Rosta material confirms this. Collett (1911–12) found that *Clethrionomys rutilus* stops in September in Norway, and much of his material was collected further south. Wildhagen (1953) found that breeding in *Microtus oeconomus*, caught further south in Norway, ends gradually in September.

It is unlikely that the breeding season starts at an earlier date in the north, because of the later persistence of the winter snow, and it must therefore be shorter. In spite of this it was evident that a proportion of the young born earlier in the season reach maturity and may breed before the end of the season. Wildhagen (1953) stated that in the mountain districts of south Norway, the voles normally have only one generation a year. He did find occasional specimens, however, which evidently were young of the same year and were in breeding condition.

This collection from the north is too small to establish with certainty that a higher proportion of young voles reach maturity and breed at a comparatively early age. For this to be so, they would either have to grow at a faster rate than the southern animals, or they would have to reach maturity while comparatively small. The former alternative may be true. If it is, then, ignoring the possibility of there being a difference in metabolism, there must be a more abundant food supply, for which there is no real evidence. The second alternative is shown to be true by reference to the body

weights. Wildhagen (1953) caught *Clethrionomys rufocanus*, *Microtus agrestis* and *M. oeconomus* in Øyer and Eidfjord some $7\frac{1}{2}$ and $8\frac{1}{2}°$ of latitude, or about 520 and 600 miles, further south in Norway. Corresponding specimens of these three species caught at Rosta all fell in the lower part of the weight-range of his animals. The one mature female *Clethrionomys rufocanus* in this collection was an extreme example; all of Wildhagen's specimens were at least two-thirds heavier.

Brambell (1935) described a collection of *Sorex araneus* made in England and Wales. This consisted of animals which were in general heavier than the Rosta specimens. This was clearly so in the case of the males, where his material caught in July and August consisted of sexually mature animals most of which weighed 11 g or more and of immature animals weighing 10 g or less. The Rosta material consisted of mature animals weighing 8 g or more and of immature animals weighing 6·5 g or less. These comparisons also show that in general even the older animals are still comparatively under weight at the end of the breeding season, when they might be expected to be at their heaviest after several weeks of summer feeding. Dale (1940) noticed a similar phenomenon in *Microtus pennsylvanicus* and other American species of *Microtus*. He found that the size increases from north to south. The reason for this is still open to speculation.

Sterile oestrous cycles had occurred in some of those *Microtus oeconomus* which had recently attained maturity, and in all of those which had been breeding since the beginning of the season. Similar cycles had occurred in all those *Clethrionomys rutilus* which had recently attained maturity, but there is no evidence of their occurrence in the older females. The single specimen of female *Clethrionomys rufocanus* which was caught had recently attained maturity and had passed through one sterile cycle before becoming pregnant. Brambell & Rowlands (1936) found that female *C.* (*Evotomys*) *glareolus* of England undergo a varying number of sterile oestrous cycles at the beginning of the breeding season, but later on most become pregnant again at the post-partum oestrus without the intervention of sterile cycles. Young females which attain maturity during the course of the season frequently become pregnant at the first oestrus. These comparisons show that sterile oestrous cycles are commoner in the older *Microtus oeconomus* and in the young *Clethrionomys rutilus* than in *C. glareolus* of England. Because these cycles are commoner in different age-groups of *Microtus oeconomus* and *Clethrionomys rutilus* of north Norway, it is difficult to ascribe an adaptive feature to this character.

The finding of two specimens of *Microtus oeconomus* which had ovulated but which plainly had not copulated, since there were no spermatozoa in the vagina and uterus, is of interest since it was contrary to the work of Bodenheimer & Sulman (1946) on *M. guentheri*. They stated: 'The vole (*Microtus*) belongs to the rabbit-ferret-cat group of animals, in which ovulation normally occurs only in consequence of copulatory stimulation.' Two of their specimens were found to be in proestrus, with cornified plugs in the vagina, although they had been isolated from males for 50 days after weaning. Both were found to have quills of wheat in the uterus. No such foreign bodies were found in the two specimens from Rosta which had ovulated.

The average number of embryos in *Microtus oeconomus* was 7·50. The material caught by Wildhagen (1953) in July and August in areas farther south in Norway had

an average number of 5·80 at Øyer and of 5·44 at Eidfjord. Application of the *t* test shows that the differences between his material and the Rosta collection are probably significant. The average number of embryos in *Sorex araneus* was 7·75. Brambell (1935) found an average of 6·45 in England and Wales. He did not give sufficient data for it to be possible to test the significance of this difference with a *t* test. Application of Student's *t* test, taking the material he caught throughout the season as the parent population, shows that the average number of embryos in the Rosta material is again probably significantly greater.

These comparisons indicate that at least some of the small mammals of arctic Norway tend to have larger litters than those from farther south. The voles tend to start breeding in the season of their birth, at a comparatively early age; but the shrew, *S. araneus*, does not attain maturity until the following season, either in the north or south. These tendencies towards a greater intensity of breeding seem to be off-set by a greater frequency of sterile oestrous cycles, which occur between pregnancies in some and before first copulation in others. These tendencies are still further off-set by the comparative shortness of the breeding season in the north.

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SUMMARY

1. A collection of small mammals was made at Rosta in arctic Norway during July and August 1953.

2. The following species were trapped: *Sorex araneus*, *Neomys fodiens*, *Clethrionomys rutilus*, *C. rufocanus*, *Microtus agrestis* and *M. oeconomus*.

3. Their reproductive organs were examined and the sexual activity determined.

4. The breeding season is shorter, the adults are smaller and more juveniles reach precocious maturity than in the south.

5. Sterile oestrous cycles are frequent in newly mature *Clethrionomys rutilus* and in older *Microtus oeconomus*.

6. There is a tendency towards larger litters than in the south.

7. Seven specimens of *M. oeconomus* were used for a study of the oestrous cycle by direct examination of vaginal smears.

8. The cycle is similar to that in laboratory rats and mice, but differs in that (*a*) leucocytes often persist into full oestrus, and (*b*) proestrus may not be followed by oestrus, but this is possibly an indication of an approaching end to the breeding season.

9. The periodicity of the cycle ranged from about six to eleven days, with an average of 8½ days.

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THE FAUNA LIVING IN STOUPE BECK SANDS, ROBIN HOOD'S BAY (YORKSHIRE, NORTH RIDING)

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(With 3 Figures in the Text)

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INTRODUCTION

Robin Hood's Bay (see map, Fig. 1), about five miles south of Whitby, extends for about two and a half miles from North Cheek to South Cheek (or Ravenscar); the bay is probably nowhere more than five fathoms deep, and is fully exposed to winds from the east and north-east. At the village of Robin Hood's Bay there is a small laboratory belonging to Leeds University, which was put freely at our disposal on a number of occasions by Professor Spaul, and we would like to express our deep gratitude to him for his kindness in so doing.

The foreshore of the whole bay is predominantly rocky, the rock being mainly blue lias. In some places, especially north of the laboratory, there are considerable areas of smooth, level rock with very little growing or living on it, but round most of the bay the rock is arranged in slightly tilted strata which form a wide anticline. The arrangement below the laboratory is typical, where between high-water neaps and low water springs there is a series of thirteen scars, each one with a gentle landward slope and a vertical or overhanging seaward face. At the base of some of these faces there is a certain amount of sand, and it was from this habitat that Dennell (1933) obtained his material when he worked out the swimming, burrowing and feeding mechanisms of the amphipod *Haustorius arenarius* (Slabber).

The whole bay is backed by cliffs of lias surmounted by boulder clay, and there are three permanent streams: King Beck at Robin Hood's Bay Village, Mill Beck half a mile south, and Stoupe Beck half a mile south again. In front of each beck there is a beach of sand extending from about high-water neaps to below tide-marks.

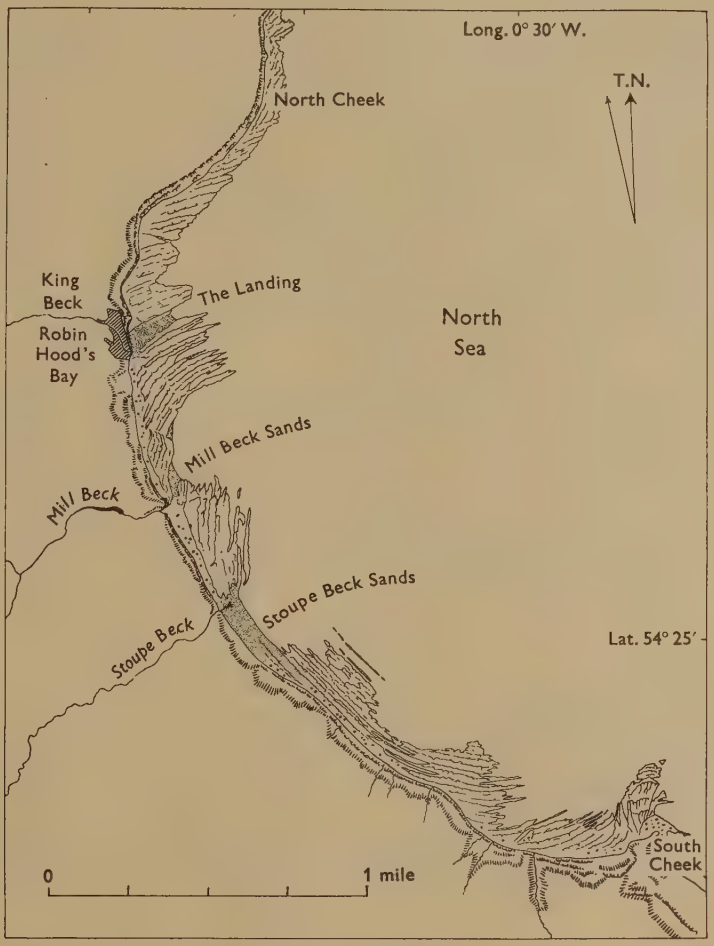

Fig. 1. Map of Robin Hood's Bay, showing the position of Stoupe Beck Sands. (By permission of H.M.S.O.)

The sands at King Beck, which are known as The Landing, are the closest to the laboratory, but for various reasons we decided not to concentrate on them. The sand is often very shallow, only a matter of inches above the rock, and the whole sandy area is small. Furthermore, in 1947, and again in 1948, the sand was remarkably barren; this was almost certainly due to the very severe winter of 1946–47, when for

some weeks there had been large pieces of ice washing up and down with the tide and churning up the sand. Since 1948, however, there has developed a rich polychaete fauna including *Arenicola marina* L., *Nephthys hombergii* Aud. & M.-Ed. and *N. cirrosa* Ehlers, *Nerine cirratulus* (Della Chiaje) and *N. foliosa* (Aud. & M.-Ed.), *Scolelepis fuliginosa* (Claparède) and *Capitella capitata* (Fabr.).

Mill Beck Sands are extensive and deep, but take on a marked S-bend which makes it impossible to lay out straight (and easily repeatable) lines of sampling; levelling, too, is rendered difficult by the distance and inaccessibility of the nearest bench mark.

Stoupe Beck Sands are the farthest from the laboratory; this involved the carrying of all gear for a mile each way along the shore (or along the top of the cliffs when the tide was in), but was amply compensated for in other ways. The sand is deep, and fairly stable except in rough weather; the shape of the beach is roughly rectangular, measuring about 200 yd from high-water mark to low-water mark and about 250 yd from side to side; the beck runs down one side of the beach and does not influence the water in the sand more than a few yards away (see p. 438); and, finally, levelling was made easy by the presence of a bench mark on the abutment of a footbridge, only 14·2 ft above ordnance datum, and visible from the top of the beach itself some 50 yd away.

The extreme range of the tide at Robin Hood's Bay is about 19 ft (Admiralty Tide Tables), the mean springs range being given as 15·3 ft, mean neaps range 8 ft, and least neaps range 6 ft; the time of high-water at full and new moon is 0355 G.M.T., which means that good low tides occur at about noon. The tides are thus very similar to those at Plymouth. The sand at Stoupe Beck extends from HWN to below tide-marks; sometimes it stretches up to HWS after heavy weather, but usually there is a shingle bank from HWN to the foot of the cliffs.

METHODS

(*a*) *Scope*

In 1949 one line of samples was taken at 10-pace intervals down a traverse (Traverse 1) from the top of the sand to LWS. In 1950 the same line of samples was repeated (but with smaller samples), and a second traverse (Traverse 2) was worked 35 yd south of Traverse 1. Two short lines of samples (Offsets 1 and 2) were worked from the beck out to the sand. The salinity of the interstitial water was measured roughly from Traverse 1 and accurately from the offsets, and samples of the sand were taken for mechanical analysis. All positions on both traverses were accurately levelled to 0·1 ft.

(*b*) *Traverse* 1

From a conspicuous, and apparently permanent, boulder at the edge of Stoupe Beck at about mean sea-level, 47 paces on a bearing from the Nab at Mill Beck (half a mile away) placed one at right angles to a rectangular boulder imbedded in the cliff of boulder clay. This spot was marked with a stone, and the traverse was then marked out with stones at 10-pace intervals up or down from this spot (which was 50 paces down the traverse) on a bearing from the boulder in the cliff (70° mag.). One of us (J. S. C.) did all the pacing, so as to keep the unit as constant as possible. In 1950

Traverse 1 was repeated, and Traverse 2 laid out 35 paces south of Traverse 1. This method was fast and accurate; by a system of cross-bearings taken in 1949, we found that 160 paces down Traverse 1 in 1950 was within a yard of 160 paces in 1949.

(*c*) *Sieves*

Several previous surveys of sand faunas have used sieves with meshes as coarse as 2 mm, which allow the smaller polychaetes and most of the amphipods to escape. Watkin (1942), however, used a sieve with 30 meshes to the inch, and we did the same. In order to prevent the accumulation of coarse material in the sample we made a pair of sieves, one fitting inside the other. The inner sieve consisted of copper sheet with $\frac{1}{8}$ in. holes, and this retained gravel, adult *Haustorius* and all but the smallest *Nephthys*, but very little else; the outer sieve was made of 30 in. mesh copper gauze, whose openings were about $\frac{1}{2}$ mm across, and this retained *Nerine* and all stages of *Bathyporeia* and *Pontocrates* except perhaps for newly hatched *P. norvegicus* Boeck. It also retained a good deal of sand, sometimes as much as 3 lb jars full from one sift. This limited the amount of sampling that could be done in one day, as all this sand had to be carried back to the laboratory to be examined as follows: the sand was placed in a flat dish and just covered with sea water; formalin was added, on which all living animals came to the surface and could be pipetted off; by then shaking the dish any dead animals could be brought to the surface, and by gentle rocking could be made visible against the sand.

(*d*) *Sampling*

Our samples were confined to the top inch or two of sand; the sand is very wet, and to have taken accurate deeper samples would have consumed more time than could be spared; a hole dug in the sand at any level on the shore filled up with water immediately. According to Watkin (1942), 90% of *Bathyporeia* and almost all *Pontocrates* live in the surface inch, whereas *Haustorius arenarius* and *Nerine cirratulus* tend to live deeper down; we therefore probably missed a good many of the latter two species.

Four spades-full of sand to a depth of $1\frac{1}{2}$–2 in. filled the inner sieve, and this made up a unit of '1 sift'. In five trials the area of 1 sift was found to vary only slightly, from 320 to 336 sq.in., average 326 sq.in. 326 sq.in. is approximately 2·3 sq.ft, or 0·2 sq.m. At all stations down Traverse 1 at least five sifts, or 1 sq.m, were taken in 1949; in 1950 only one sift was taken at each station on Traverses 1 and 2, and similarly at the two offsets by the beck; in these samples the numbers of animals have been multiplied by 5 and expressed as numbers per square metre.

THE SAND

Samples of the surface sand were collected down Traverse 1 at 0, 20, 50, 80, 110, 140 and 170 paces, and were graded mechanically by Dr A. J. Southward at Port Erin, to whom we wish to express our thanks. He used the same method as in his work on the beaches in the Isle of Man (Southward 1953), dividing the sand into the following grades:

Gravel. > 2 mm, by sifting.

Coarse sand. 2·0–0·2 mm, by sifting.

Fine sand. 0·2–0·02 mm, by sedimentation through a 10 cm column of water for 4 min 48 sec at 20° C.

Silt and clay by difference of weight (i.e. all material smaller than 0·02 mm).

A salt correction was applied on the basis of a water content of 25 % and a salinity of 35‰, which gives 0·17 g of salt in 20 g of dry sand, and the percentage composition by weight is given in Table 1, where the Kames Bay sand (Watkin 1942) is included for comparison. The two beaches are both characterized by the predominance of the coarse sand fraction, but whereas at Kames Bay there is less fine sand and more silt farther up the shore, at Stoupe Beck these two fractions remain fairly constant. On the other hand, there is virtually no gravel at Kames Bay, whereas at Stoupe Beck there is a good deal of it above mean sea-level. These differences do not seem to be very large, and both strands can be called 'coarse sand beaches'; nevertheless, as will be shown later (p. 441), there are very large quantitative differences between their faunas.

Their essential similarity is brought out in Table 2, where comparative analyses are given of seven traverses of five beaches, arranged in descending order of exposure to wave action. The scale of exposure is an arbitrary and, admittedly, a rather subjective one, extending from 0 for complete enclosure to 10 for Stoupe Beck Sands which is undoubtedly the most exposed of the series. It is based partly on Southward's (1953) analysis of exposure factors on Manx shores, partly on the knowledge by one of us of all the beaches concerned, and partly on a consideration of the geographical relationships between the beaches and the neighbouring land and the likely set and strength of the waves. The most protected beaches consist mainly of fine sand, the more exposed of coarse sand (except for Port Erin D), and the others are intermediate. Kames Bay sand is closer in texture to Stoupe Beck sand than are any of the others; since our methods of collecting animals were deliberately modelled to some extent on those of Watkin (1942) at Kames Bay, this similarity of texture of beach makes a real comparison of the two faunas all the more possible.

As has been mentioned, Stoupe Beck Sands are wet, with the water-table virtually at the surface at all levels below HWN. This water was tested by means of a hydrometer at intervals down the traverse, and its salinity was always within two parts per thousand of that of the sea. On parts of other beaches, e.g. Port Erin (Pirrie, Bruce & Moore 1932) and Kames Bay (Smith 1955), the salinity of the interstitial water may be markedly less than that of the sea.

THE FAUNA

(*a*) *Traverse* 1 (1949)

Samples were taken at 10-pace intervals down this traverse on various dates from 2 July to 17 July; at least five sifts (equal to a sample of 1 sq.m.) were made at each position, and the fauna of the top inch or two is expressed in numbers per square metre in Table 3. It will be seen that these methods were somewhat rough, but then so is the distribution of the animals, which varies both from time to time and from place to place, as will be shown later. Far more time would have been consumed than truth gained had greater precision of collection been attempted. As it was, we are confident

Table 1. *Mechanical analysis (percentage by weight) of sand at Stoupe Beck and at Kames Bay*

At these two places the depth of sand sampled, and the size-range of animals collected, were very similar.

	Stoupe Beck Sands (present investigation) Paces down traverse							Kames Bay, Millport (Watkin 1942) Station no.				
	0	20	50	80	110	140	170	10	19	28	34	42
Tidal levels (approx.)	MHWN	EHWN	MSL+	ELWN	MLWN		MLWS	HWN+	MSL		LWN+	
Gravel, >2 mm	0·5	17·8	2·6	2·5	0	0	0·1	0	0	0	0	0
Coarse sand, 2·0–0·2 mm	87·6	74·8	89·2	86·6	87·6	87·6	86·5	95·4	96·4	96·4	89·7	90·5
Fine sand, 0·2–0·02 mm	10·4	8·6	7·5	10·3	11·5	11·1	11·5	0·7	1·6	2·4	8·9	8·1
Silt and clay, +error	1·5	0·8	0·7	0·6	0·9	1·3	1·8	3·9	2·0	1·2	1·4	1·4

Table 2. *Mechanical analysis (percentage by weight) of sands from seven traverses of five beaches, arranged in descending order of exposure to wave action*

The first four lines give the average for stations evenly spaced down the whole beach; the last four lines give comparative figures for roughly the same level in each case. In the two Port Erin sets of samples the 'coarse sand' fraction measured from 2 to 0·25 mm, and the 'fine sand' fraction measured less than 0·25 mm.

	Traverse						
	Stoupe Beck I	Port Erin, I.O.M.* D	Kames Bay, Millport†	Derbyhaven, I.O.M.‡ C	Derbyhaven, I.O.M.‡ A	Port Erin, I.O.M.* A	Port St Mary, I.O.M.‡ C
Exposure factor	10	8	7	4	2	2	<1
No. of samples	7	5	5	10	12	5	9
Depth sampled	1 in.	20 cm	1 in.	5 cm	5 cm	20 cm	5 cm
Average of whole traverse							
Gravel, >2 mm	3·3	16·5	0	5·1	9·5	0·2	0·2
Coarse sand, 2·0–0·2 mm	85·6	25·5	93·7	53·4	67·6	6·2	6·0
Fine sand, 0·2–0·02 mm	10·1	58·0	4·3	41·6	20·7	93·6	88·3
Silt and clay, +error	1·0	ignd.	2·0	0·4	2·2	ignd.	5·5
Reading between MSL and LWN							
Gravel, >2 mm	0	12·3	0	0	0·1	0	0
Coarse sand, 2·0–0·2 mm	87·6	30·2	96·4	49·6	71·7	7·0	1·8
Fine sand, 0·2–0·02 mm	11·5	57·5	2·4	50·4	24·7	93·0	94·4
Silt and clay, +error	0·9	ignd.	1·2	0	3·5	ignd.	3·8

* Pirrie, Bruce & Moore 1932. † Watkin 1942. ‡ Southward 1953.

Table 3. *Stoupe Beck Sands, Traverse 1 (1949): total fauna, in numbers per square metre*

Tide-marks (approx.) ...	EHWN				OD			EHWN	MLWN								MLWS		
Paces down traverse ...	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	
Height in ft above C.D.	11·3	10·4	9·6	9·0	8·1	7·5	6·8	6·0	5·3	4·7	4·0	3·7	3·3	3·0	2·5	2·0	1·3	0·7	Total
Haustorius arenarius	10	51	98	48	7	13	2	—	—	—	2	—	—	—	—	—	—	—	231
Bathyporeia sarsi	—	74	194	158	67	50	7	5	—	—	—	1	—	—	—	—	—	—	556
B. pelagica	—	1	1	81	68	100	64	85	94	73	178	213	15	11	—	5	1	—	990
B. elegans	—	—	—	—	—	—	—	—	—	—	1	1	2	1	2	—	6	—	13
B. guilliamsoniana	—	—	—	—	—	—	—	—	—	—	1	1	4	3	5	4	6	4	28
Pontocrates norvegicus	—	18	7	66	121	42	154	272	204	84	59	46	10	25	3	9	1	—	1121
P. arenarius	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	3	13	17
Total Amphipoda	10	144	300	353	263	205	227	362	298	157	242	262	31	40	10	18	17	17	2956
Nematoda	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
Nemertini	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	—	3
Phyllodoce maculata	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Eteone longa	—	1	—	1	—	—	1	—	—	1	3	—	—	—	—	—	—	—	7
Nereid (*juv.*)	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Nephthys cirrosa	—	—	—	—	—	2	4	3	1	2	1	3	—	6	—	4	3	—	29
N. longosetosa	—	—	—	—	—	—	—	3	5	2	4	—	5	5	5	3	10	5	47
Nerinides cantabra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	1	—	5
Nerine cirratulus	—	8	3	15	9	20	4	5	2	1	2	5	—	—	—	—	2	—	76
Spio filicornis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Paraonis fulgens	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
Arenicola marina	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—	3
Anomalocera patersoni	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	2
Parathemisto oblivia	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Eurydice pulchra	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Megalopa	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Lacuna vincta	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Grand total	10	153	306	370	274	227	237	375	307	164	253	271	36	52	15	31	35	22	3138

that neither the area nor the volume of any 'sift' varied by more than 10% from those of any other.

The whole traverse was accurately levelled from a bench mark 14·2 ft above ordnance datum on the northern pier of the footbridge across Stoupe Beck (ordnance datum is 7·9 ft above chart datum at Robin Hood's Bay). Fig. 2 shows the profile of the shore down Traverse 1, the positions of the sifts, and the tidal levels, all relative to chart datum. The slope was nearly uniform from HWN to LWS, except for a slight levelling off between LWN and MLWS.

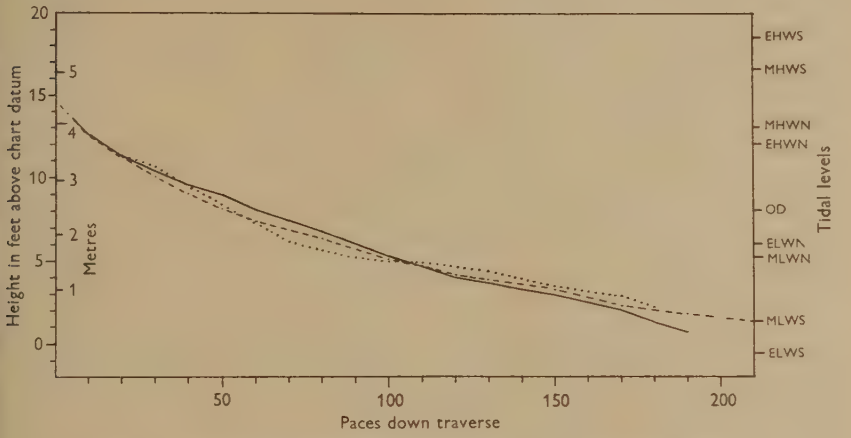

Fig. 2. Stoupe Beck Sands, profiles of traverses. ——, Traverse 1 (1949); - - - - -, Traverse 1 (1950); ....., Traverse 2 (1950).

Table 3 shows that the fauna was dominated by the amphipods, which provided 2956 out of a total of 3138 animals. Of the other 182, most were polychaetes: 76 *Nerine cirratulus* distributed from EHWN to between low-water neaps and springs, 47 *Nephthys longosetosa* Oersted from ELWN to MLWS, and 29 *N. cirrosa* from below MSL to MLWS. The other animals occurred only in ones and twos, even such a typical shore animal as the isopod *Eurydice pulchra* Leach being rare; all of them, however, were probably true inhabitants of the sand, except for *Anomalocera patersoni* Templeton, *Parathemisto oblivia* (Kröyer), the megalopa, and *Lacuna vincta* (Montagu), which had presumably been stranded by the tide. The samples produced three small tails of *Arenicola marina*, but no adults; there are a good many of the latter in Stoupe Beck Sands, but they are not dense and rarely, if ever, amount to more than two or three per square metre. Low down, there are many *Ammodytes* sp. which our sampling method failed to catch, and one was seen to emerge from the sand as high up as MLWN. (Two specimens were examined by Mr A. B. Bowers, and proved to be *A. lanceolatus* Lesauvage.) We found no sign of either lamellibranchs or echinoderms.

The amphipods consisted of seven species: *Haustorius arenarius*, four species of *Bathyporeia* and two of *Pontocrates*. *P. norvegicus* was the most abundant, extending from EHWN to MLWS with a maximum of 272 per square metre at ELWN; at Stoupe Beck, at any rate, it seems to be confined to between tide-marks, and only just overlapped

with *P. arenarius* (Bate) which is mainly subtidal. Of the species of *Bathyporeia*, *B. guilliamsoniana* (Bate) and *B. elegans* Watkin live mainly below tide-marks, but also extended in small numbers nearly up to low-water neaps. *B. pelagica* (Bate) and *B. sarsi* Watkin are both intertidal and fairly abundant. *B. pelagica* had the same vertical range as *Pontocrates norvegicus*, but whereas the latter had its maximum at about ELWN, *Bathyporeia pelagica* was densest well below MLWN, with a maximum of 213 per sq.m, and was more evenly distributed throughout its range. *B. sarsi* had a very restricted vertical range in 1949, and was virtually confined to between EHWN and ELWN, with a pronounced maximum of 194 per sq.m near the top of its range; there were still 74 per sq.m in the highest sample at which it occurred. Finally, *Haustorius arenarius* occupied much the same levels as *Bathyporeia sarsi*, with a maximum of 98 per sq.m between MSL and EHWN. No animals were found on Traverse 1 in 1949 higher than 20 paces down the traverse.

Since our sieve retained the youngest stages of all these amphipods (except perhaps for some of the newly hatched *Pontocrates norvegicus*), the opportunity was taken to count the sexes and their developmental stages, and the results are shown in Table 4. In all except *Haustorius* the adult males are distinguished by their very long antennae with many segments; in the immature males the antennae show proliferation of segments without, at first, any great increase in length, the change from the last immature moult to the first adult one being very marked. Adult females carry eggs or at any rate have fully-developed oostegites with long bristles; immature females have developing oostegites, from the merest buds to those of full size but without bristles. Juveniles show no secondary sexual characters. In *Haustorius* the males have no secondary sexual characters (Watkin 1941) and can be distinguished from females only by the absence of oostegites; 'juveniles' include all *Haustorius* smaller than any that show oostegites.

In the case of *Bathyporeia elegans*, *B. guilliamsoniana* and *Pontocrates arenarius* the numbers were too small to show very much; in *Haustorius* the numbers of males and females were about equal, but in the remaining three species females were markedly more numerous than males, the approximate ratios of females to males being: *Bathyporeia sarsi* 7:4, *B. pelagica* 5:1, and *Pontocrates norvegicus* 3:2. Within each sex there are curious differences in the proportion of immature to mature specimens. Among females the proportions are roughly *Bathyporeia sarsi* 2:5, *B. pelagica* 1:1, and *Pontocrates novegicus* 1:1, while among males the corresponding ratios are 2:5, 2:1 and 5:2. Corresponding figures for Kames Bay (Watkin 1942) are *Bathyporeia pelagica* 9 females to 5 males, *B. elegans* 11:10, and *Pontocrates norvegicus* 3:1; again females in general markedly outnumbered the males. As will be shown in a subsequent paper (Colman & Segrove 1955), however, males tend to outnumber females among those swimming in the tidal plankton at night.

(*b*) *Traverse* 1 (1950) *and Traverse* 2 (1950)

In July 1950 Traverse 1 was repeated; as was mentioned earlier, a system of cross-bearings on distant landmarks enabled us to be certain that every sample down this traverse in 1950 was taken from within a yard of the corresponding sample in 1949.

Table 4. *Stoupe Beck Sands, Traverse 1 (1949): details of amphipod population, in numbers per square metre*

Tide-marks (approx.)	EHWN			MSL				ELWN	MLWN							MLWS			Total (each sex)
Height in ft above C.D.	11·3	10·4	9·6	9·0	8·1	7·5	6·8	6·0	5·3	4·7	4·0	3·7	3·3	3·0	2·5	2·0	1·3	0·7		
Paces down traverse	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	Total	
Haustorius arenarius																				
Juveniles	—	17	45	43	6	10	2	—	—	—	1	—	—	—	—	—	—	—	124	—
Females, adult	} 10	34	{22	5	—	2	—	—	—	—	—	—	—	—	—	—	—	—	(29)	(29)
Males, adult			{31	—	1	1	—	—	—	—	1	—	—	—	—	—	—	—	(34)	(34)
Total	10	51	98	48	7	13	2	—	—	—	2	—	—	—	—	—	—	—	231	—
Bathyporeia sarsi																				
Juveniles	—	24	67	77	43	39	7	5	—	—	—	—	—	—	—	—	—	—	262	—
Females {immature	—	14	20	11	2	4	—	—	—	—	—	—	—	—	—	—	—	—	51	} 187
Females {adult	—	21	72	35	6	2	—	—	—	—	—	—	—	—	—	—	—	—	136	
Males {immature	—	6	15	4	3	1	—	—	—	—	—	—	—	—	—	—	—	—	29	} 107
Males {adult	—	9	20	31	13	4	—	—	—	—	—	1	—	—	—	—	—	—	78	
Total	—	74	194	158	67	50	7	5	—	—	—	1	—	—	—	—	—	—	556	—
B. pelagica																				
Juveniles	—	—	—	36	26	44	41	22	26	23	51	64	—	2	—	2	—	—	337	—
Females {immature	—	—	—	13	14	15	9	39	35	21	51	71	—	1	—	—	—	—	269	} 538
Females {adult	—	1	—	14	13	22	12	21	26	25	56	52	15	8	—	3	1	—	269	
Males {immature	—	—	1	16	13	10	2	3	6	2	10	17	—	—	—	—	—	—	80	} 115
Males {adult	—	—	—	2	2	9	—	—	1	2	10	9	—	—	—	—	—	—	35	
Total	—	1	1	81	68	100	64	85	94	73	178	213	15	11	—	5	1	—	990	—
B. elegans																				
Juveniles	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—
Females {immature	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	} 5
Females {adult	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	—	4	
Males, adult	—	—	—	—	—	—	—	—	—	—	—	1	2	—	2	—	2	—	7	7
Total	—	—	—	—	—	—	—	—	—	—	1	1	2	1	2	—	6	—	13	—
B. guilliamsoniana																				
Females, adult	—	—	—	—	—	—	—	—	—	—	—	1	2	3	—	3	4	2	15	15
Males, immature	—	—	—	—	—	—	—	—	—	—	1	—	2	—	5	1	2	2	13	13
Total	—	—	—	—	—	—	—	—	—	—	1	1	4	3	5	4	6	4	28	—
Pontocrates norvegicus																				
Juveniles	—	—	—	7	25	6	34	27	39	18	5	7	—	6	—	4	—	—	178	—
Females {immature	—	—	—	7	20	6	38	79	72	17	17	16	—	4	—	2	—	—	278	} 567
Females {adult	—	15	7	40	54	22	38	49	23	9	13	5	5	5	3	—	1	—	289	
Males {immature	—	—	—	9	17	4	28	78	57	34	19	17	—	8	—	3	—	—	274	} 376
Males {adult	—	3	—	3	5	4	16	39	13	6	5	1	5	2	—	—	—	—	102	
Total	—	18	7	66	121	42	154	272	204	84	59	46	10	25	3	9	1	—	1121	—
P. arenarius																				
Females {immature	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	3	} 17
Females {adult	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2	10	13	
Total	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	3	13	17	—
Grand total	10	144	300	353	263	205	227	362	298	157	242	262	31	40	10	18	17	17	2956	—

At the same time samples were taken from a similar traverse laid out 35 paces south of Traverse 1, and the results of these two series are shown in Table 5, all figures for Traverse 2 being shown in italics. In 1950 we had not time to take more than one sift from each level; in Table 5 the numbers have been multiplied by 5 to make them equal to those in 5 sifts or 1 sq.m, and so comparable with the 1949 figures. This treatment admittedly makes the 1950 figures somewhat rough, and they are more valuable in showing the range occupied by each species than in giving the numbers present; nevertheless, when the numbers differed markedly between Traverses 1 and 2 (in the cases of *Bathyporeia sarsi* and *Pontocrates norvegicus* for example) they did so with some consistency right down the shore, and this makes us feel that the figures do have some significance. Both 1950 traverses were accurately levelled, and the resulting profiles are shown in Fig. 2, together with that of the 1949 profile of Traverse 1. The levels at any one point never differed by as much as one foot on Traverse 1 between 1949 and 1950, and the same is true as between Traverses 1 and 2 in 1950.

When the results from the two 1950 traverses are compared, certain features in the distribution are at once obvious. Although the traverses were only 35 paces apart, in the case of several species there was a large difference in numbers in the two traverses. Thus there were 20 times as many *Haustorius* in Traverse 1 as in Traverse 2, 4 times as many *Bathyporeia sarsi* and 1·5 times as many *B. pelagica*; on the other hand, Traverse 2 produced 1·5 times as many *Pontocrates norvegicus*, the most abundant amphipod on either traverse. This latter species made up one-third of the total in Traverse 1, but two-thirds in Traverse 2. Nevertheless, the vertical distribution in the two traverses was much the same, and in none of these four species did the range in the less densely populated traverse extend significantly above or below the limits occupied in the other traverse. It seems that the distribution of these animals is more patchy in a horizontal than in a vertical sense.

The polychaete genus *Nephthys* occurred in small numbers over a large part of both traverses, and *Nerine cirratulus* was quite abundant with, on Traverse 1, a maximum of 160 which was remarkable for being as high up on the shore as HWN (15 and 20 paces down the traverse). 'Other polychaetes' (the term includes several species occurring in ones and twos) were more generally distributed, and more numerous, on Traverse 2.

Of the other animals in the 1950 traverses, the only noteworthy ones were the larvae and pupa-cases of diptera. These are believed to have come from the drift-weed above high-water mark which was swarming with these maggots. On each traverse there was a marked maximum at 3 ft above chart datum, between low-water neaps and springs. It is difficult to see how they had been removed from their drift-weed and then concentrated in such a narrow zone so far down the shore. The larvae seemed none the worse for their translation, and were actively wriggling in the sand.

(*c*) *Traverse* 1 *in* 1949 *and* 1950

As far as the amphipods were concerned, there was much less difference between samples taken a year apart on Traverse 1 than there was between Traverses 1 and 2 as sampled contemporaneously in 1950. *Haustorius arenarius*, *Bathyporeia sarsi*, *B. elegans*, *B. guilliamsoniana*, *Pontocrates norvegicus* and *P. arenarius* were all more

Table 5. *Stoupe Beck Sands, Traverses 1 (1950) and 2 (1950): total fauna, in numbers per square metre*

In 1950 only one sift of approximately 0·2 sq.m was taken at each level, and the numbers of animals have been multiplied by 5. *All data on Traverse 2 are in italics.* N.S. = no sample.

Tide-marks (approx.)				MHWN		EHWN			MSL				ELWN		MLWN										MLWS		
Height in ft above C.D.	Trav. 1	14·7		12·6		11·2		10·1	9·1	8·2	7·5		6·4		5·1	4·9	4·1	3·9		3·3		2·3		1·8	1·6		
	Trav. 2	*14·5*		*12·6*		*11·1*		*10·7*				*6·2*		*5·2*	*5·0*			*4·4*		*3·5*		*2·9*	*2·2*				
Paces down traverse	... ...	0	5	10	15	20	25	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	Total
Haustorius arenarius	Trav. 1	—	—	—	50	25	15	135	40	40	75	45	5	—	—	—	—	—	—	—	—	—	—	—	—	—	430
	Trav. 2	—	—	—	—	—	*5*	—	*10*	—	*5*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*20*
Bathyporeia sarsi	Trav. 1	—	—	—	30	5	5	65	165	135	175	120	15	5	10	10	15	20	5	5	—	—	—	—	—	—	785
	Trav. 2	—	—	—	—	—	—	—	*10*	*35*	*15*	*5*	*25*	*50*	*30*	*5*	*15*	—	*5*	—	—	—	—	—	—	—	*195*
B. pelagica	Trav. 1	—	—	—	—	—	—	—	10	10	65	95	30	25	40	30	100	20	15	15	5	5	—	—	—	—	465
	Trav. 2	—	—	—	—	—	—	—	—	*10*	*15*	*20*	*40*	*65*	*45*	*40*	*20*	*15*	*5*	*10*	*20*	*10*	—	—	—	—	*315*
B. elegans	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	20	25	25	20	10	5	—	30	5	160
	Trav. 2	—	—	—	—	—	—	—	—	—	—	—	*10*	—	*5*	*15*	*15*	—	*5*	*20*	*20*	*40*	*35*	*15*	—	—	*180*
B. guilliamsoniana	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	5	5	—	15	—	5	—	35	10	85
	Trav. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*5*	—	—	—	*10*	*15*	*20*	*15*	*15*	—	—	*80*
Pontocrates norvegicus	Trav. 1	—	—	—	5	15	80	40	145	120	35	75	95	65	105	40	190	110	130	60	15	35	10	—	25	—	1395
	Trav. 2	—	—	—	—	*10*	*15*	*25*	*25*	*360*	*100*	*100*	*150*	*260*	*255*	*240*	*300*	*95*	*160*	*40*	*35*	*50*	*15*	*15*	—	—	*2250*
P. arenarius	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	5	—	—	—	—	—	5	185	200
	Trav. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*35*	—	—	*35*
Total Amphipoda	Trav. 1	—	—	—	85	45	100	240	360	305	350	335	145	95	155	90	330	175	185	105	55	50	20	N.S.	95	200	3520
	Trav. 2	—	—	—	—	*10*	*20*	*25*	*45*	*405*	*135*	*125*	*225*	*375*	*335*	*305*	*350*	*110*	*175*	*80*	*90*	*120*	*65*	*80*	*N.S.*	*N.S.*	*3075*
Nephthys spp.	Trav. 1	—	—	—	—	—	5	—	—	—	—	15	—	—	5	10	10	20	15	10	10	—	15	—	35	5	155
	Trav. 2	—	—	—	—	—	—	—	*10*	*5*	*5*	*10*	*5*	*15*	*5*	—	*5*	*5*	*5*	*10*	*10*	*20*	*10*	*15*	—	—	*135*
Nerine cirratulus	Trav. 1	—	5	5	65	160	30	20	70	25	65	65	30	15	45	20	30	5	15	15	—	—	5	—	—	—	690
	Trav. 2	—	—	—	*35*	*20*	—	*5*	*75*	*110*	*50*	*10*	*15*	*45*	*25*	*10*	*5*	*5*	*10*	—	—	—	—	—	—	—	*420*
Other Polychaeta	Trav. 1	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	15	—	20	15	55
	Trav. 2	—	—	—	—	—	—	*10*	—	*5*	*20*	*10*	*25*	*20*	*10*	*5*	*35*	*10*	*10*	*10*	—	*15*	*15*	*10*	—	—	*210*
Diptera: larvae	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	10	130	85	5	—	5	5	250
	Trav. 2	—	—	—	—	—	—	*10*	—	*5*	—	—	*5*	—	—	—	*5*	*40*	*5*	—	*650*	*25*	—	—	—	—	*745*
Diptera: pupa cases	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	55	90	—	—	—	5	165
	Trav. 2	—	—	—	—	—	—	*5*	*15*	*150*	*5*	—	*15*	—	*80*	—	*30*	*80*	—	—	*10*	*350*	*40*	—	—	—	*780*
Diptera: imagines	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
	Trav. 2	—	—	—	*5*	—	—	—	—	—	—	—	—	—	—	—	—	—	*5*	—	—	*15*	—	—	—	—	*25*
Ammodytes sp.	Trav. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	5	10
	Trav. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*0*
Others	Trav. 1	—	—	10	—	—	—	—	5	—	—	—	—	—	—	—	—	20	—	5	15	—	—	—	—	5	75
	Trav. 2	—	—	—	*20*	*10*	—	—	*5*	—	—	—	—	—	*5*	—	—	—	—	*5*	—	*20*	—	*10*	—	—	*75*
Grand total	Traverse 1	0	5	15	150	205	135	260	435	330	420	415	175	110	205	120	370	220	225	160	265	225	80	N.S.	155	240	4920
	Traverse 2	*0*	*0*	*0*	*60*	*40*	*20*	*40*	*150*	*540*	*365*	*160*	*270*	*475*	*380*	*400*	*395*	*165*	*325*	*110*	*110*	*1190*	*155*	*115*	*N.S.*	*N.S.*	*5465*

numerous in 1950, and only *Bathyporeia pelagica* was less abundant, but even so the total number of amphipods in 1950 outnumbered those in 1949 by only 7 to 6 (3520 to 2956). Changes of this order of magnitude after as long a period as a year do not seem at all surprising. The vertical range occupied by each species was very similar in the two years, and so were the levels of maximum density, as is shown in Table 6, the heights being in feet above chart datum. There was a tendency for a species to occupy a somewhat wider range in the year in which it was more abundant; this is shown clearly by *Haustorius* and *Bathyporeia sarsi* in 1950 and by *B. pelagica* in 1949, and also by *Nerine cirratulus* in 1950.

Table 6. *Stoupe Beck Sands, Traverse 1 (1949 and 1950): the upper and lower limits, and maximal levels, of amphipods*

Heights are given in feet above chart datum, and *all data for 1950 are in italics*. A figure in brackets denotes an isolated occurrence separated by a gap from the main population of the species concerned.

		Highest sample	Maximum density	Lowest sample
Haustorius arenarius	1949	11·3	10·4 to 9·0	6·8 (4·0)
	1950	*11·9*	*10·1*	*6·4*
Bathyporeia sarsi	1949	10·4	10·4 to 7·5	6·0 (3·7)
	1950	*11·9*	*10·1 to 7·0*	*3·3*
B. pelagica	1949	10·4	7·5 and *c.* 4·0	1·3
	1950	*9·1*	*7·0 and 4·1*	*2·3*
B. elegans	1949	4·0	Extend below tide-marks	
	1950	*4·1*		
B. guilliamsoniana	1949	4·0		
	1950	*4·6*		
Pontocrates norvegicus	1949	10·4	6·8 to 5·3	1·3
	1950	*11·9*	*9·1 to 3·6*	*1·6*
P. arenarius	1949	(4·0) 1·3	Extends below tide-marks	
	1950	*(4·1) 1·6*		

The pattern of distribution of these animals on the shore at Stoupe Beck is shown in Fig. 3. In the lowest sample in each year *Pontocrates arenarius* makes an appearance. In 1949 there were 13 per sq.m at 190 paces down the traverse at 0·7 ft above chart datum; in 1950 the lowest sample was at 1·4 ft above chart datum but 20 paces farther away from land (owing to a small shift in the level of the sand (see Fig. 2)), and produced 185 per sq.m. It seems possible that in the case of this predominantly subtidal species the actual position may be more important than the exact tidal level in fixing its upper limits, and that the greater length of Traverse 1 in 1950 enabled us to get nearer the main habitat of *P. arenarius*.

(*d*) *The beck and the sand*

As already mentioned earlier (p. 430), the salinity of the interstitial water was nearly constant over the whole of Traverse 1 in 1949, and approximated to that of sea water. In 1950 we made a few observations on the salinity and fauna in the immediate neighbourhood of the beck itself, with somewhat confusing results. Two offsets, each of four samples, were made on lines at right angles to the beck, at points level with

50 and 80 paces down Traverse 1, or at about MSL and ELWN. At 50 paces on Traverse 1 there were plenty of *Haustorius arenarius*, *Bathyporeia sarsi* and *Pontocrates norvegicus*, and a few *Bathyporeia pelagica*, and also some of the polychaete *Nerine cirratulus*. At 80 paces there were few if any *Haustorius*, a few *Bathyporeia sarsi*, some *B. pelagica* and *Nerine*, and plenty of *Pontocrates*. We would have liked to make an offset level with 120 paces, where there were maxima of *Bathyporeia pelagica* and *Pontocrates norvegicus*, but at this level the beck spread out in a thin sheet so that it was impossible to decide where it began and where it ended. At the 50- and 80-pace offsets the left (northern) side of the beck was bounded by rocks, and the right bank by sand, the

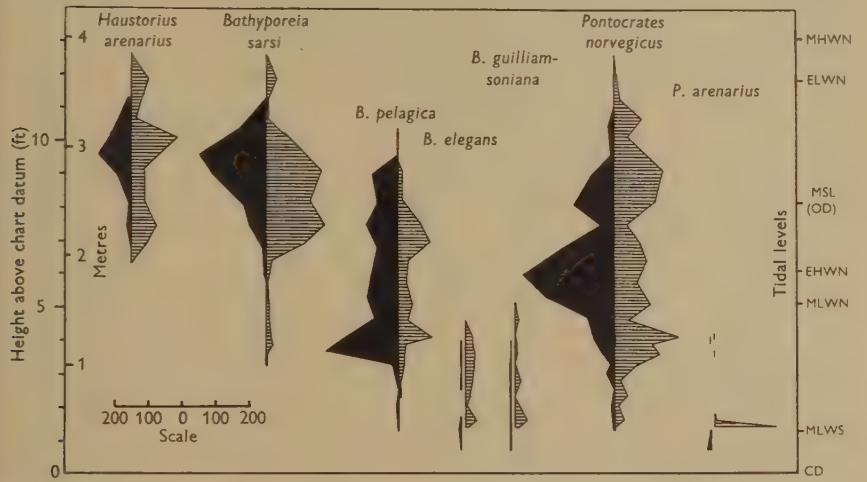

Fig. 3. Stoupe Beck Sands, Traverse 1: vertical distribution of Amphipoda in 1949 (black) and in 1950 (parallel lines) expressed in numbers per sq. m. The 1949 figures are from a minimum of 5 sifts (or 1 sq.m approx.) at each level; in 1950 only one sift was made at each level, and the numbers of animals have been multiplied by 5.

beck being about 4 ft wide and running swiftly. A sample was made in the beck by damming it until a sandbank appeared in mid-stream, and the sift was made in this sandbank. The other samples in each offset were taken at 2, 5 and 10 paces from the centre of the beck; at each position one sift was made in the same way as on the traverses, and the numbers of animals multiplied by 5 to make them equivalent to samples from 1 sq.m. At each sift a sample of interstitial water was taken and these, together with one from the sea taken at the same time, were analysed for salinity by Mr J. D. Jones, to whom we wish to express our thanks. The results from these offsets are given in Table 7.

The salinity of the sea was 35·14‰, and in offset 2 this figure was about reached by the interstitial water within 10 paces of the edge of the beck. Further up, at offset 1, the influence of the beck was a little more apparent, but even here there was far less difference between 2 and 10 paces from the beck than between 2 paces and the beck-bottom itself. It is probable that at offset 1 the beck had no influence on the interstitial water more than 20 paces away (less than half the distance to Traverse 1). The anomaly

of the salinity in the beck-bottom being higher at offset 1 than at the lower offset 2 is probably due to the fact that the dams were not made with any precision; all that these two readings show is that the beck does affect its immediate bed, but not sufficiently to make the interstitial water completely fresh.

In offset 1 the fauna consisted almost entirely of *Haustorius* and *Bathyporeia sarsi*, which both showed a marked increase away from the beck, *Haustorius* indeed doing so with almost diagrammatic precision. In the 5- and 10-pace samples, too, *Bathyporeia pelagica* and *Pontocrates norvegicus* made an appearance, though both were absent

Table 7. *Stoupe Beck Sands, offsets 1 and 2 (1950) at right angles to the Beck: total fauna, expressed in numbers per square metre*

Only one sift of approximately $\frac{1}{8}$ sq.m was taken at each position, and the numbers of animals have been multiplied by 5.

Salinity of sea, 35·14 ‰	Offset 1, level with 50 paces on Traverse 1; about MSL — Paces away from beck				Offset 2, level with 80 paces on Traverse 1; about ELWN — Paces away from beck			
	0	2	5	10	0	2	5	10
Salinity of interstitial water (‰)	13·0	29·8	33·0	33·7	3·6	34·1	35·0	35·1
Haustorius arenarius	5	25	190	375	40	35	—	25
Bathyporeia sarsi	210	200	390	780	45	80	20	15
B. pelagica	—	—	20	10	5	95	25	10
Pontocrates norvegicus	—	—	10	40	10	5	—	10
Orchestia sp. (imm. ♀)	5	5	5	5	—	—	—	—
Total Amphipoda	220	230	615	1210	100	215	45	60
Nereidae (juv.)	—	5	5	—	—	—	—	—
Nerine cirratulus	—	—	—	10	5	10	20	60
Arenicola marina (juv.)	—	—	—	—	—	—	5	—
Diptera (larvae)	—	—	—	—	—	—	5	—
Total	220	235	620	1220	105	225	75	120

from the beck itself and from the 2-pace sample. *Nerine cirratulus*, also, was found only in the 10-pace sample. In each sift on this offset there was one immature female *Orchestia*; the nearest source for this genus was a large population of *O. gammarella* (Pallas) in the shingle above high-water mark. No *Orchestia* were taken in any of the samples on the traverses themselves.

In offset 2 the picture was far less clear. *Nerine cirratulus*, it is true, increased steadily from a minimum in the beck to a maximum 10 paces away, but *Bathyporeia sarsi* and *B. pelagica* both had a maximum at 2 paces and decreased in number farther away from the beck. The mere presence of *Haustorius* was surprising, as the samples were level with the very bottom of its range on Traverse 1, and equally surprising was the scarcity of *Pontocrates norvegicus* which should have been fairly abundant. It is obvious that more work is needed before the effect of fresh water on the sand-fauna can be assessed; but that Stoupe Beck is large enough to have some influence is probably shown by the frequent occurrence below boulders to the north of the beck of the amphipod *Melita palmata* (Montagu); the occurrence of this amphipod is usually taken as an indication of fresh water influence.

COMPARISON WITH FAUNAS IN OTHER SANDY BEACHES

Quantitative surveys have been made on several sandy shores in the last twenty years or so, but in many cases the sieves used have been too coarse to catch most of the species characteristic of Stoupe Beck Sands, and this makes only rough qualitative comparison possible. In other cases, such as Holme's (1949) survey of some muddy sand in the Exe estuary, both the ecological conditions and the grade of sand were widely different from those at Stoupe Beck.

At Kames Bay, so ably surveyed by Watkin (1939, 1942) and others (notably Stephen (for references see Watkin 1942)), the grading of the sand, the angle of slope and the degree of exposure are not very dissimilar from the same factors at Stoupe Beck; our methods, too, were deliberately modelled to some extent on those of Watkin in order to make the quantitative and qualitative comparison as close as possible. Before doing this, an important reservation must be made. Watkin's surveys were made in March and early April, ours in July, and there is a certain amount of rather vague evidence in the literature about the possibility of seasonal changes in the distribution of faunas in sand. An example of this was provided by *Haustorius arenarius* at Stoupe Beck, for in April 1950 its largest numbers were farther down the shore than they had been in the previous July. There is not enough evidence on which to assess this seasonal factor and it will not be further considered here, but its possible importance should not be ignored.

The most obvious difference between Kames Bay and Stoupe Beck Sands is the very much greater richness of the former both in species and in individuals. *Tellina tenuis* da Costa is really abundant at Kames Bay below HWN, and on Watkin's traverse it reached a maximum density of 7000 per sq.m, mostly in the surface inch of sand. Watkin also recorded six other species of lamellibranch in one's and two's, together with several *Echinocardium cordatum* (Pennant) at and below LWN. We, on the other hand, did not find a single lamellibranch or echinoderm of any species in Stoupe Beck Sands.

Polychaetes at Stoupe Beck were represented mainly by *Nerine cirratulus*, *Nephthys cirrosa* Ehlers and *N. longosetosa*. At Kames Bay *Nerine cirratulus* and *Nephthys caeca* (O. F. Müller) occurred in somewhat larger numbers at much the same levels, the similarity in distribution of *Nerine cirratulus* on the two shores being striking; in each place it occurred from HWN nearly to LWS, but had its maximum density high up in its range, just below HWN. A few other polychaete species occurred in very small numbers at Stoupe Beck, but at Kames Bay there were several more abundant than those mentioned above, such as *Ophelia cluthensis* McGuire (with a maximum density of some 200 per sq.m), *Nereis diversicolor* O. F. Müller, *Scolelepis ciliata* (Keferstein), *Phyllodoce groenlandica* Oersted, and others less numerous.

Crustacea tell much the same story. At Stoupe Beck amphipods made up the entire crustacean population except for one or two specimens of the isopod *Eurydice pulchra*. One species, *Bathyporeia sarsi*, did not occur at Kames Bay. The most abundant Stoupe Beck amphipod was *Pontocrates norvegicus*, with a maximum of 360 per sq.m, and the largest total number of amphipods at any one station was only 405. At Kames Bay the most abundant amphipod was *Bathyporeia pilosa*

Lindström (not found at Stoupe Beck) which at and above HWN reached the astonishing density of 17000 per sq. m., or about 12 per sq. in. *Pontocrates norvegicus* was about 10 times as numerous at Kames Bay as at Stoupe Beck, *Bathyporeia elegans* about 40 times or more, and *B. guilliamsoniana* about 3 times. *Pontocrates arenarius* extends farther up the shore at Kames Bay, to above LWN, and overlaps *P. norvegicus*; at Stoupe Beck, although our lines of sample seem to have reached a little lower than that of Watkin, we only just touched the upper limits of the former species, and it hardly overlapped at all with *P. norvegicus*.

In view of this regular superiority of Kames Bay, the numbers of *Haustorius arenarius* are of some interest. The distribution is much the same on both beaches, with a maximum rather high up (just above EHWN at Kames Bay but just below at Stoupe Beck) and with occasional specimens down to about MLWN, and for once the numbers were much the same in the two beaches, with maxima of 98 and 135 on Traverse 1 (1949 and 1950) and 220 at Kames Bay. Since *Haustorius* was shown by Watkin to occupy the deeper levels of the sand (two-thirds of them more than 3 in. down) we probably missed a good many at Stoupe Beck, so it is probable that in this species we had the only one present in both beaches which was actually more numerous at Stoupe Beck than at Kames Bay. (It is impossible to be sure of this, because of the patchiness of *H. arenarius*; in 1950 Traverse 1 produced 430 altogether, compared with only 20 in Traverse 2, while Watkin only sampled one line of stations.)

The amphipod *Urothöe brevicornis* Bate, which we have not recorded anywhere from Robin Hood's Bay, was present in fair numbers at Kames Bay from high water neaps to Watkin's lowest sample; it was more numerous there than was any species at Stoupe Beck. The isopod *Eurydice pulchra*, of which we dug up two specimens only, was at Kames Bay rather more numerous than *Haustorius* and had a very similar distribution, with a maximum just below EHWN near the top of its range and occasional individuals down to LWN. Finally, Watkin obtained fair numbers of two cumaceans, *Cumopsis goodsiri* (van Beneden) and *Pseudocuma cercaria* (van Beneden) from the sand in the lower part of his traverse. Both of these are mainly subtidal species, but extended farther up the shore than *Bathyporeia elegans*, *B. guilliamsoniana* or *Pontocrates arenarius*. At Stoupe Beck we dug up all these last three amphipods, but not a single cumacean; one of Watkin's two species is known to occur at Stoupe Beck, however, for we have obtained *Pseudocuma cercaria* in the night tidal plankton over the beach (Colman & Segrove 1955).

On the whole, the species common to Stoupe Beck Sands and Kames Bay occupy similar zones on the two beaches, except that *Pontocrates arenarius* extends a good deal higher up the beach at Kames Bay, where it overlaps with *P. norvegicus*. On some other beaches there are more striking differences. Jones (1948) records both species of *Pontocrates* as extending from MSL down to shallow water below tide marks on Manx shores, with *P. norvegicus* extending farther down and preferring muddier sand than does *P. arenarius*; Crawford (1937) gives them a similar distribution in the south-west of England, but adds that he never caught them together. At Stoupe Beck, on the other hand, *P. norvegicus* appeared to die out above ELWS, and it extended well above MSL, but at the two or three stations where it overlapped with *P. arenarius* the two species were caught in the same sifts.

Haustorius arenarius occurs above MSL at Stoupe Beck and at Kames Bay, but at LWM in Devon and Cornwall according to Crawford (1937).

Eurydice pulchra, a cyrolanid isopod, can apparently have its level of maximum distribution almost anywhere on the shore. The two specimens at Stoupe Beck were in neighbouring stations between MSL and HWN; at Kames Bay (Watkin 1942) its maximum was at and above MSL; Crawford (1937) records it in Devon and Cornwall from MSL downwards; Holme (1949) in the Exe estuary from MHWN; Pirrie, Bruce & Moore (1932) at Port Erin, I.O.M., from above MSL, and Southward (1953) from below MLWN at Derby Haven, I.O.M., the latter place being only six miles from Port Erin.

The above facts deserve some comment in the light of a recent paper of great interest by Dahl (1952). In this paper Dahl has outlined a scheme of ecology and zonation on sandy shores of universal, world-wide application, to correspond with the similar scheme for rocky shores designed by T. A. and A. Stephenson (1949). Dahl's 'subterrestrial fringe' is dominated by scavengers: talitrid amphipods in temperate regions and ghost crabs (*Ocypode*) in the tropics; with this there seems no reason to disagree. Dahl's 'midlittoral zone' is dominated by cyrolanid isopods (such as *Eurydice pulchra*) both in temperate and tropical regions; in the beaches discussed in this paper, *Eurydice* is sometimes abundant in this zone, but usually only over a narrow belt, the position of which can vary from above MSL to below LWN even on quite neighbouring beaches. At Stoupe Beck *Eurydice* did not dominate at all. Dahl's 'sublittoral fringe' is dominated in the tropics by hyppid crabs, and in north temperate regions by amphipods of the families Haustoriidae and Oedicerosidae. On the beaches discussed in this paper the haustoriid *Bathyporeia pilosa*, when present, is apt to be the most abundant crustacean on the shore, but lives at and above HWN (Watkin 1942, Holme 1949); the midlittoral zone both at Kames Bay and Stoupe Beck is clearly dominated by haustoriids and by *Pontocrates norvegicus*, in spite of the fact that Dahl specifically mentions the latter as characteristic of the sublittoral fringe. At Stoupe Beck, at any rate, the only crustacea that can be reasonably assigned to the 'sublittoral fringe' are *Bathyporeia elegans*, *B. guilliamsoniana* and *Pontocrates arenarius*.

Indeed, the region near low-water mark in Stoupe Beck Sands is a conspicuously barren one for invertebrates of all kinds, and affords the greatest contrast to similar levels on the nearby rocks where, at the top of the laminarian zone, there are many species in large numbers. This, together with the variation not only in the specific make-up and relative numbers on different beaches, but also in the actual habitats of several species, make it seem that caution is needed before attempting to apply Dahl's scheme to British beaches.

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SUMMARY

1. In July 1949 and 1950 the fauna was examined in the top inch or so of Stoupe Beck Sands (Robin Hood's Bay, Yorkshire) between tide-marks. The sand was coarse, the beach exposed to strong wave action and the fauna poor.

2. The dominant group was amphipods of the genera *Haustorius*, *Bathyporeia* and *Pontocrates*, and the numbers were counted of juveniles and of immature and adult males and females.

3. In 1950, below low-water neaps, there were a good many dipterous larvae and pupae, which had presumably come from the drift-weed above high-water mark.

4. There were some polychaetes mainly of the genera *Nephthys* and *Nerine*, but no lamellibranchs or echinoderms.

5. A preliminary investigation was made of the influence of the fresh water of the beck on the salinity and fauna of the beach; it was found to be negligible 20 paces from the beck.

6. Comparison has been made with the faunas in sandy beaches elsewhere.

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THE TIDAL PLANKTON OVER STOUPE BECK SANDS, ROBIN HOOD'S BAY (YORKSHIRE, NORTH RIDING)

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(With 1 Figure in the Text)

In 1930 Elmhirst (1932) made a number of experimental hauls with a medium tow-net at the water's edge on a sandy beach. Two years later these were followed up by further hauls (Elmhirst 1932) taken at intervals of a few hours and designed to test the influence of the moon on and also seasonal differences in the composition of the plankton. Still later, during the 12-month period from January to December 1936, an extensive set of hauls was taken at fairly regular intervals. This last set was subsequently the subject of a detailed analysis by Watkin (1939, 1941). With the exception of this work little serious attempt (apart from that of Liao (1951)) appears to have been made to investigate the nature of the plankton of the intertidal zone, though both Elmhirst and Watkin indicated the necessity for further work of this type.

The work recorded in this paper had to be carried out in a restricted period of time and was thus more limited in its scope than Elmhirst's later work. On the other hand, it was hoped that by using the bottom plankton trawl with double nets described below it would be possible to obtain more precise information regarding the vertical distribution of the plankton, and further that by taking several sets of hauls at short intervals of time and at different states of the tide more information could be obtained regarding the extent to which different species invade the intertidal zone. These expectations have been fulfilled, and as a result it has been possible to make a tentative analysis of the factors influencing the composition of the intertidal plankton. The work is by no means complete for, as Watkin (1941) points out, it is almost impossible to obtain simultaneously the various sets of data which are required. As, however, there is no immediate prospect of the work being further extended it seems desirable to publish the results so far obtained.

APPARATUS AND METHODS

By fitting a stramin net inside the mouth of an Agassiz trawl Russell (1928) showed how different is the plankton close to the bottom from that in mid-water. More recently, Bossanyi (1951) and Wickstead (1953) have devised more elaborate plankton trawls fitted with opening and closing devices so that uncontaminated samples can be obtained from the bottom layers when fishing in deeper waters. Inevitably these trawls are on the heavy side and intended for power hauling, and one at least needs handling by means of a derrick. The apparatus described below is simpler than either

of these recently devised trawls, for it was primarily intended for use in very shallow water, in particular the surf on a sandy beach, and we were not concerned with the fitting of any closing mechanism. Our main aim was to produce an apparatus light enough to be man-hauled, preferably by one person. In this we were successful, though it is probable, in the light of experience, that the weight could have been still further reduced with no loss in performance. A novel feature of the apparatus is the fitting of two superposed nets which enabled us to investigate the stratification of the plankton in a very narrow depth zone.

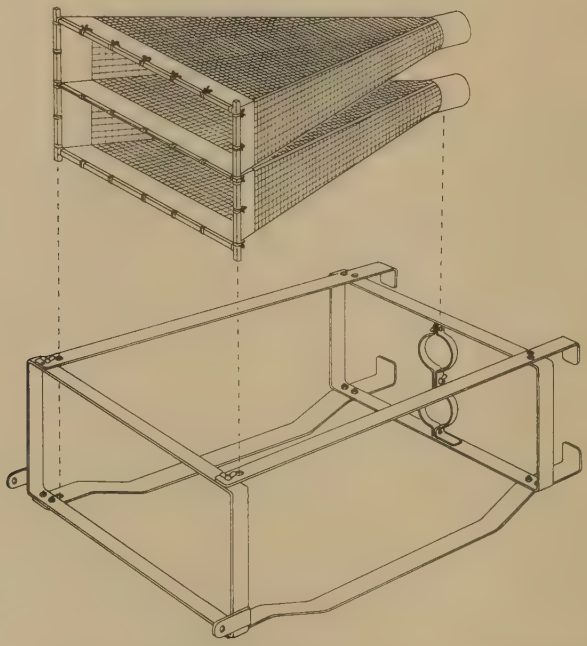

Fig. 1. Bottom plankton apparatus showing (above) the twin net-assembly and (below) the framework into which it fits.

The complete trawl comprises two quite separate assemblies as shown in Fig. 1: a framework manufactured of steel strip and heavily galvanized, and a net assembly comprising a rectangular brass frame carrying the two plankton nets with their collecting jars. The framework consists essentially of two rectangular frames (subsequently referred to as the front and rear frames) bolted together by four longitudinal strips along the upper and under sides near the corners. The four strips fit flush to the front edge of the front frame but extend for 4 in. beyond the rear frame, and a further 2 in. or so on each strip is bent inwards at right angles to form a foot. This allows the apparatus to stand vertically with the rear frame well clear of the ground, the position adopted when the collecting jars are being removed or changed. The upper strips are made of $1\frac{1}{2} \times \frac{1}{4}$ in. material, whilst the pair beneath the frames are broader ($2 \times \frac{1}{4}$ in.) since they serve as the runners on which the trawl is dragged; this lower pair are shaped

as depicted in Fig. 1 so that the frames are lifted some 2 in. clear of the ground, giving ample clearance between the nets and the ground on sandy bottoms. Paired nuts and bolts are used at all junctions except where the upper strips are bolted to the front frame. Here single wing bolts are used, providing a simple quick-release arrangement for the rapid insertion or removal of the net assembly. Holes, $\frac{1}{2}$ in. diameter, and drilled through each of the four strips immediately to the rear of the front frame, are so aligned as to receive the projecting lugs on the brass frame of the net assembly. The front and rear frames are constructed from $1\frac{1}{2} \times \frac{1}{4}$ in. strip, bent to shape and welded, the actual dimensions being: front frame 2 ft $3\frac{3}{4}$ in. $\times$ 1 ft $1\frac{1}{2}$ in., rear frame 2 ft 3 in. $\times$ 1 ft $\frac{3}{4}$ in. The smaller size of the rear frame permits it to fit comfortably inside the front frame for ease in storage and transport. The front frame carries two forwardly projecting lugs, $3\frac{1}{2} \times 1\frac{1}{2} \times \frac{1}{4}$ in., welded to the lower ends of the frame sides and drilled to receive the shackles which attach the towing bridle. The rear frame is fitted centrally with a clamping device which holds the collecting jars at the rear ends of the two nets. The device is built of two separate lengths of light strip ($1 \times \frac{1}{8}$ in.), so shaped that when fitted together they form two circular clamps 3 in. apart and equidistant from the rear frame, each with an internal diameter of about $3\frac{1}{2}$ in. One side of the device is welded to the rear frame by its bent-over ends, and the other half is bolted to it by means of three bolts fitted with wing nuts placed as shown in Fig. 1. Adjustment of these bolts permits the rapid clamping or release of the collecting jars. In practice it was found necessary to bind the sides of the ring clamps with twine to ensure a snug fit and a secure grip. The dimensions of the framework are as follows: overall length, 3 ft 8 in.; width, 2 ft $3\frac{3}{4}$ in.; height, 1 ft 4 in. It weighs approximately 42 lb.

The rectangular frame, to which the collecting nets are directly attached, is made from $\frac{1}{2}$ in. square brass rod and carries at each corner a vertically placed lug $\frac{3}{4}$ in. long. The corners of these lugs are rounded off so that they slide easily into the holes drilled for their reception in the main trawl framework. The aperture of the frame is divided horizontally by a bar $\frac{1}{4}$ in. thick brazed to the sides of the frame, the two apertures thus formed being each 24×6 in., giving each net a collecting area of 1 sq. ft. The two nets are identical. The mouth of each is rectangular, 24×6 in., and is formed of a 2 in. canvas band which carries some twenty pairs of tapes for attachment to the brass frame. The net itself is of 30-mesh bolting silk; it is rectangular in section with strengthening tapes down the corner seams, and tapers down to a cylindrical canvas sleeve at the cod end. The size of the sleeve is such as to fit a 1 lb. honey jar which is used as a collecting bucket. The overall length of the nets is 3 ft. $3\frac{3}{4}$ in. Assembling the complete trawl is a very simple operation. The wing bolts on the front frame are unscrewed and the lower lugs of the brass frame, the nets being already attached, are fitted into the holes drilled through the runners. Pushing the brass frame up to the front frame springs the upper lugs into the holes in the upper strips which are then bolted back into position. It remains to stand the trawl on its rear end, fit the nets with collecting jars and clamp them to the rear frame. The overall weight of the apparatus is approximately 50 lb, and though this is somewhat on the heavy side one person, wading through shallow water on a sandy beach, can tow the trawl steadily at a rate of 1–$1\frac{1}{2}$ m.p.h.

The results recorded in this paper are based on material collected in June and July 1949 by means of this bottom trawl. On each occasion the trawl was hauled by one person at the end of a long tow-rope for a distance of 100 yd (except for some of the daytime hauls) along a line parallel with the shore, the distance being measured off by a second person on the beach. The speed of towing varied somewhat according to the prevailing conditions but fell within the limits of 1–1½ m.p.h. Every endeavour was made to keep the trawl immersed in a constant depth of 2 ft of water so that, knowing the time of each haul, the height of the haul in reference to chart datum could be calculated from the predicted tidal data (Admiralty Tide Tables 1949). Since the beach had already been accurately surveyed in connexion with the investigation of the sand fauna (Colman & Segrove 1955) it was then possible to calculate the position of the haul on the beach. As will be shown later, this facilitated comparison of the tow-net samples with the infauna of the beach.

All material was preserved initially in 5% sea-water formalin and later identified as opportunity offered. Identification and nomenclature are based on the following:

Amphipoda: Chevreux & Fage (1925), Sars (1895–1921), Sexton & Spooner (1940) (*Marinogammarus*), Spooner (1951) (*Gammarus*), Watkin (1938) (*Bathyporeia*).

Isopoda: Sars (1895–1921).

Cumacea: Fage (1951).

Mysidacea: Tattersall & Tattersall (1951).

Copepoda: Sars (1895–1921).

Pycnogonida: Bouvier (1923).

Polychaeta: Fauvel (1923, 1927).

RESULTS

(*a*) *Day hauls*

A single series of daylight hauls was made on 26 June 1949 in bright sunny conditions with a calm sea. The first haul was made at 1005 G.M.T. at low water of a good spring tide, the remaining hauls following at approximately hourly intervals as the tide rose. On several occasions the nets rapidly became choked with drifting weed, mainly fragments of *Laminaria*, and these hauls in consequence were curtailed. The resulting variation in the length of the hauls may be seen by reference to Table 1, but, despite this range, the main features of the results are so obvious that it has not been necessary to express the individual catches in terms of a haul of unit length. (In the night hauls made later we were fortunately not bothered by drifting weed.)

Table 1 gives, in a somewhat condensed form, the results of this series of hauls. Examination of the table clearly shows that the catches in the upper five hauls (hauls 2–6) were extremely poor, much as had been expected. On two occasions one or other of the nets was empty and only rarely did more than one specimen of any species occur in a particular haul. It may be added that both the immigrants from the subtidal zone and the intertidal sand forms—mainly species of *Bathyporeia* and *Pontocrates*—were present in very small numbers in comparison with the night hauls. The first haul, however, was in striking contrast, being much richer both in species and in numbers; it was comparable in fact with some of the night hauls (cf. Table 5).

In particular, the numbers of the subtidal amphipods (*Apherusa* spp. and *Nototropis swammerdami* (M.-Edw.) being the most important), juvenile *Idotea baltica* and the cumacean *Bodotria scorpioides* (Montagu) were of the same order as those in night hauls. Mysids, too, though fewer, were present in appreciable numbers; the notable absence of *Schistomysis spiritus* Norman, and the very small number of crab megalopas, largely account for the difference between the day and night figures. This marked difference between the lowest haul and the upper five hauls is somewhat surprising. The result suggests that some species at least are relatively indifferent to a high light

Table 1. *Day hauls, 26 June 1949*

The hauls were taken on a rising tide, low water having occurred at 0955 G.M.T.

Haul no.	1	2	3	4	5	6
Time (G.M.T.)	1005	1115	1215	1315	1400	1445
Height above chart datum (ft)	−1·0	+1·5	4·0	7·0	9·5	10·5
Height above chart datum (m)	−0·3	+0·5	1·2	2·1	2·9	3·2
Length of haul (yd approx.)	150	50	35	100	80	100
Apherusa spp.	13	1	—	—	—	—
Nototropis swammerdami	90	4	—	—	1	—
Other subtidal Amphipoda	9	1	1	—	—	—
Intertidal sand Amphipoda	1	—	—	2	7	6
Praunus flexuosus and *P. inermis*	16	1	—	—	—	—
Leptomysis lingvura	10	1	—	—	—	—
Bodotria scorpioides	6	—	—	—	1	—
Idotea spp. (mainly *I. baltica*)	16	3	—	—	—	—
Carcinus maenas megalopas	7	2	1	4	10	3
Other Decapoda	8	—	—	1	—	—
Gastropoda	29	2	—	—	—	—
Others	9	—	—	—	2	3
Total	214	15	2	7	21	12

intensity, but at the same time raises the problem of why they fail to penetrate further into the tidal zone in daylight. It should also be pointed out that the first day haul, at 1 ft below chart datum, was nearly 2 ft lower than the lowest night haul. These points will be discussed later.

(*b*) *Night hauls*

Four series of night hauls were made between 4 and 12 July 1949, and the relevant tidal and other data are shown in Table 2. The catches from these fifteen night hauls amounted to a total of 4149 animals (omitting fish eggs and fragments of hydroids and polyzoa), and included no less than eighty-two species, mostly crustacea. There were thirty-three species of amphipods, six of cumaceans, five of copepods, eight of mysids, four of isopods, seven of decapods, nine of pyconogonids, nine of polychaetes and one species of oligochaete. Most of these species were represented by only one or very few specimens, and the catches as a whole were characterized by the relative abundance of a few species rather than by the regular occurrence of many. This is shown in Table 3. Those species marked with an asterisk inhabit the sand over which the net was hauled, and none of these was really abundant in the surf plankton.

There are three ways in which the data from the different hauls can be arranged: (1) By the time of day irrespective of date; this method produces a random distribution

of figures and obscures any significant data there may be; we have therefore not used it. (2) By order of haul (i.e. in the same order as the list of hauls in Table 2); this has proved useful for those species which normally live off-shore and which migrate or drift into the intertidal zone with the tide (see below, p. 454 and Table 5). (3) By

Table 2. *Night plankton hauls made in 1949*

	Time of LW (G.M.T.)	No. of haul	Time of haul (G.M.T.)	Height above C.D. (ft)	Height above C.D. (m)	Sea conditions	Tidal conditions
4 July	1648	1	2210	10·8	3·3	Very little swell	Hauls just before and at HW
		2	2300	11·3	3·4		
8–9 July	2049	1	2210	1·9	0·6	Moderate surf	Hauls on rising tide
		2	2255	3·5	1·1		
		3	2340	5·7	1·7		
		4	0025	8·0	2·4		
		5	0110	10·2	3·1		
10–11 July	2221	1	2202	1·0	0·3	Calm; no swell	Hauls at LW and on rising tide
		2	2242	0·8	0·2		
		3	2325	1·3	0·4		
		4	0007	2·8	0·9		
12–13 July	2340	1	2200	4·0	1·2	Very calm	Hauls on falling tide
		2	2242	2·2	0·7		
		3	2320	1·5	0·5		
		4	0000	1·3	0·4		

height of haul relative to chart datum; this is the best method for dealing with those species which actually live in the sand over which the net was dragged (Table 4). Tables 4 and 5 give the data concerning the thirty-three most abundant species, i.e. those which occurred five or more times, or of which there were at least three in

Table 3. *Total numbers caught of the ten most abundant species, and percentage of the total catch*

		Percentage of grand total
Grand total	4149	
Carcinus maenas (Pennant) megalopas	1177	28% (2 spp. 52%; 3 spp. 64%; 6 spp. 81%; 10 spp. 87%)
Nototropis swammerdami (M.-Edw.)	928	
Schistomysis spiritus Norman	531	
Leptomysis lingvura (G. O. Sars)	255	
**Pontocrates norvegicus* Boeck	239	
Idotea baltica (Pallas) juv.	211	
Gammarellus homari (Fabricius)	94	
**Bathyporeia pelagica* Bate	69	
Apherus bispinosa (Bate)	68	
**Pontocrates arenarius* (Bate)	45	

any one haul. The only exception to this restriction is *Bathyporeia guilliamsoniana* (Bate) of which there were only four single specimens, but since this species will be discussed below, together with the other sand-dwelling species, it has been included in Table 4. For the sake of completeness there now follows a list of those species which occurred only four times or less, and never more than two in one haul.

Amphipoda
Amphithoë rubricata (Montagu)
Apherusa clevei G. O. Sars
A. jurinei (M.-Edw.)
Caprella linearis (L.)
Cheirocratus intermedius G. O. Sars
C. sundevalli (Rathke)
Dexamine thea Boeck
Iphimedia obesa Rathke
Jassa falcata (Montagu)
Marinogammarus obtusatus (Dahl)
Stenothoë marina (Bate)
S. monoculoides (Montagu)
Tritaeta gibbosa (Bate)
Tryphosa nanoides (Lilljeborg)
Unciola planipes Norman

Cumacea
Cumella pygmaea G. O. Sars
Diastylis sp.
Nannastacus sp.
Pseudocuma longicornis (Bate)

Copepoda
Bradypontius papillatus (Scott)
Caligus rapax M.-Edw.

Mysidacea
Gastrosaccus spinifer (Goës)
Mesopodopsis slabberi (van Beneden)
Siriella armata (M.-Edw.)

Isopoda
Idotea baltica (Pallas) (adult)
I. granulosa Rathke
I. emarginata (Fabricius) (juv.)

Decapoda
Corystes cassivelaunus (Pennant) (post-larva)
Galathea strigosa (L.) (zoea)
Eupagurus bernhardus (L.) (megalopas)
Leander sp. (larvae)

Pycnogonida
Ammothea echinata Hodge
Anoplodactylus petiolatus Kröyer
A. pygmaeus (Hodge)
Callipallene brevirostris (Johnston)
Endeis spinosa (Montagu)
Nymphon brevirostre Hodge
N. rubrum Hodge
Phoxichilidium femoratum (Rathke)
Species unid.

Polychaeta
Autolytus prolifer (O. F. Müller)
Eulalia sanguinea Oersted
Nephthys cirrosa Ehlers
Nerine cirratulus (Delle Chiaje)
Paraonis fulgens (Levinsen)
Pista maculata (Dalyell) (tubes only)
Polynoid
Scolelepis sp.

Oligochaeta
Lumbricillus sp.

In Table 4 the data for the intertidal species have been arranged in order of height of sample in the lines named 'net'. (It so happened that two hauls—10 July haul 3, and 12 July haul 4—were made at the same level of 1·3 ft above chart datum; the means of the figures for these two hauls are given in Table 4.) The other lines in Table 4, named 'sand', give the actual numbers present in the top inch or two of sand over which the net was dragged, and they were derived in the following way. The length of each haul was 100 yd or 90 m; the width of the net was 2 ft or 0·6 m; the height of the net mouth was 1 ft, or about half the depth of water. $90 \times 0{\cdot}6 \times 0{\cdot}5 = 27$, so the catch of one net haul was regarded ideally as representing the entire contents of the water over 27 sq.m of sand. Since the net tended to be in less rather than more than 2 ft of water, the figure 30 has been used instead of 27. From our previous paper (Colman & Segrove 1955) it is known approximately how many of these species per square metre live in the sand at various levels on the beach; the figures for the levels fished by the net were obtained by interpolation and multiplied by 30, and the resulting figures shown in the 'sand' lines in Table 4. (Our basis for this calculation was Traverse 1 (1949); the more sketchy data from Traverse 1 (1950) and Traverse 2 were not used.)

Two facts are at once apparent; first, that remarkably few of the individuals known to be present in the sand are caught in the plankton, and secondly that with very few exceptions the animals caught by the net came from within the range occupied by the

Table 4. *Night hauls (July 1949); the intertidal sand-inhabiting crustacea*

The lines named 'net' give the actual numbers caught in the tidal plankton; the lines named 'sand' give the equivalent numbers known to be present in the sand, as derived from Colman & Segrove (1955) (see text, p. 451).

Date, July 1949		4	4	8	8	8	12	8	10	12	8	12	10 12		10	10		
Haul no.		2	1	5	4	3	1	2	4	2	1	3	3 4		1	2		Net-
Height above chart datum	(ft)	11·3	10·8	10·2	8·0	5·7	4·0	3·5	2·8	2·2	1·9	1·5	1·3		1·0	0·8		sand
	(m)	3·4	3·3	3·1	2·4	1·7	1·2	1·1	0·9	0·7	0·6	0·5	0·4		0·3	0·2	Total	ratio
Haustorius arenarius	Net	—	—	9	3	—	—	—	—	—	—	—	—		—	—	12	1
	Sand	*300*	*900*	*1900*	*250*	—	*50*	—	—	—	—	—	—		—	—	*3400*	*283*
Bathyporeia sarsi	Net	2	1	4	15	12	—	—	3	—	—	—	—		—	2	39	1
	Sand	—	*1200*	*3120*	*1920*	*100*	—	*20*	—	—	—	—	—		—	—	*6360*	*163*
B. pelagica	Net	—	—	1	36	9	1	8	7	—	1	2	2		2	—	69	1
	Sand	—	*20*	*30*	*2150*	*2700*	*5340*	*3420*	*200*	*100*	*150*	*70*	*30*		*20*	—	*14230*	*209*
B. elegans	Net	—	—	—	—	2	—	1	—	1	—	7	3		—	—	14	1
	Sand	—	—	—	—	—	*30*	*50*	*40*	*30*	*30*	*150*	*180*		*90*	*30*	*630*	*45*
B. guilliamsoniana	Net	—	—	—	—	—	1	—	1	—	—	1	1		—	—	4	1
	Sand	—	—	—	—	—	*30*	*80*	*120*	*130*	*120*	*170*	*180*		*150*	*120*	*1100*	*275*
Pontocrates norvegicus	Net	17	14	13	62	65	24	17	6	8	2	2	2		2	2	236	1
	Sand	—	*300*	*450*	*3240*	*7290*	*1770*	*840*	*480*	*180*	*240*	*100*	*30*		*20*	—	*14940*	*63*
P. arenarius	Net	—	—	—	—	—	—	—	—	—	—	7	15		2	6	30	1
	Sand	—	—	—	—	—	*30*	—	—	—	—	*60*	*90*		*240*	*360*	*780*	*26*
Eurydice pulchra	Net	—	—	2	7	2	—	—	—	—	—	—	—		—	—	11	1
	Sand	—	—	*10*	*10*	—	—	—	—	—	—	—	—		—	—	*20*	*2*

same species in the sand; furthermore, the largest numbers caught by the net tended to be from the same levels as the maxima in the sand. The proportion of these animals in the water, as opposed to the sand, at any one time is shown in the last column of Table 4, and from this it appears that on any one tide the individuals of several of these species swim for a total of only a minute or two in several hours. *Haustorius arenarius* and three species of *Bathyporeia* are swimming for less than $\frac{1}{150}$th of the time, while *B. elegans*, *Pontocrates norvegicus* and *P. arenarius* swim for more than $\frac{1}{100}$th of the time during which the sand is covered by water. It is probable that this swimming consists of a number of very short excursions rather than of a few longer ones; when watched in the laboratory these amphipods make occasional sudden darts into the water for no apparent reason, and quickly return to the sand. Usually they return in a second or less, but sometimes they swim for a few seconds and may go several times round their tank; often they return very close to the spot from which they emerged. These habits would account for their being caught in the plankton only over the sand which they normally inhabit. Further, Table 1 shows that even this moderate amount of swimming is largely suppressed by day and is confined to the hours of darkness. There is a curious range in swimming ability among animals with such similar swimming habits. *Haustorius arenarius* is both clumsy-looking and slow, and seems built more for burrowing than for swimming; the other amphipods in Table 4, however, have elegant, streamlined forms and can swim both fast and well, at any rate over short distances.

The only other animal in Table 4, the isopod *Eurydice pulchra*, seems to be in a different category and may spend as much as half its time out of the sand when the tide is in; in the laboratory it certainly swims much more readily than the amphipods do, but its numbers in Stoupe Beck Sands were too low to make further consideration of *Eurydice* possible here.

These results and conclusions are in broad agreement with those of Watkin (1939, 1941) at Kames Bay, Millport, if allowance is made for differences in the two local faunas (see Colman & Segrove 1955); Watkin, however, never found *Haustorius arenarius* in intertidal plankton samples, in spite of its presence in the Kames Bay sand. Our results, also, tend to bear out Watkin's observations on the sex ratio of these species in the plankton as compared with that of sand samples. In general, females outnumber males in total populations of *Bathyporeia* (Colman & Segrove 1955), but in the plankton the males are the more numerous, which implies that they swim more than do the females. Watkin (1939) found that for the species of *Bathyporeia* considered together the ratio of adult males to adult females in the sand was 3:5, but that in the plankton it was 3:1. At Stoupe Beck the corresponding figures were 1:3 in sand and somewhat less than 2:1 in the plankton (due partly to a lower ratio for *B. pelagica* of 2·5:1 as against Watkin's 6:1, and to the presence in our catches of *B. sarsi* with a 1:1 ratio, which species did not occur at Kames Bay). In the case of *Pontocrates norvegicus* the males again appear to swim more than the females, but not so much so as in *Bathyporeia*; in the sand there was one adult male to every three adult females, while in the plankton the ratio was 2:3, almost the same as that found by Watkin (1941).

The first two hauls on 4 July differed from the others in several ways. They were

not only the highest up on the beach, but were also the only hauls made above mean sea-level before midnight, the first haul being made very soon after dusk and the second some 50 min later. Their catches also were the poorest in number of species, the first haul containing nothing but fifteen intertidal amphipods, forty-three *Schisto-*

Table 5. *Night hauls in July 1949: the immigrant tidal plankton*

The catches of both nets have been added together for each haul. The totals for sand amphipods are included, but have been shown in detail in Table 4. The sand amphipods add up to 403 in Table 4, but to 424 in Table 5; the discrepancy is due to two hauls both at a height of 1·3 ft (10 July haul 3 and 12 July haul 4) having been lumped together and averaged in Table 4. *Eurydice pulchra* is included in Table 5 under 'Other Isopoda'.

Tide and sea conditions	4 July HW; slight swell		8 July Rising; rather rough					10 July LW and rising; calm				12 July Ebbing; calm			
Haul number	1	2	1	2	3	4	5	1	2	3	4	1	2	3	4
Time (GMT)	2210	2300	2210	2255	2340	0025	0110	2202	2242	2325	0007	2200	2242	2320	0000
Height above chart datum (ft)	10·8	11·3	1·9	3·5	5·7	8·0	10·2	1·0	0·8	1·3	2·8	4·0	2·2	1·5	1·3
Height above chart datum (m)	3·3	3·4	0·6	1·1	1·7	2·4	3·1	0·3	0·2	0·4	0·9	1·2	0·7	0·5	0·4
AMPHIPODA															
Apherusa bispinosa	—	—	2	27	16	5	—	1	2	4	1	1	3	4	2
Calliopius crenulatus	—	—	—	3	5	1	—	—	—	—	—	—	—	4	2
Dulichia monacantha	—	—	—	—	3	1	—	—	—	1	—	1	1	1	—
Gammarellus homari	—	—	—	11	1	—	—	1	3	10	2	—	5	50*	11
Gammarus locusta and *G. zaddachi oceanicus*	—	—	5	2	9	4	13	—	1	—	1	—	—	2	1
Guernea coalita	—	—	3	7	7	5	2	—	—	1	—	—	—	—	—
Jassa falcata	—	—	—	6	4	4	—	1	—	—	—	1	2	7	5
Nototropis swammerdami	—	3	25	58	18	37	4	9	92	112	37	2	28	259	244
Parathemisto oblivia	—	—	1	—	10	1	1	—	—	—	—	—	—	—	—
Perioculodes longimanus	—	—	3	11	14	9	1	1	1	—	—	—	—	—	—
Intertidal amphipoda (Table 4)	15	19	3	26	88	116	27	6	10	6	16	26	9	19	38
Other amphipoda	—	1	1	4	4	7	—	2	5	—	2	—	1	8	2
Total Amphipoda	15	23	43	155	179	190	48	21	114	134	59	31	49	354	305
CUMACEA															
Bodotria scorpioides	—	—	3	3	5	2	10	3	—	1	—	—	1	2	1
Pseudocuma similis	—	—	1	3	1	2	1	—	1	—	—	—	—	—	—
Other cumacea	—	—	1	3	—	—	—	1	2	—	—	—	—	—	1
Total Cumacea	—	—	5	9	6	4	11	4	3	1	—	—	1	2	2
COPEPODA															
Anomalocera patersoni	—	—	—	1	4	3	2	—	—	—	—	—	—	—	—
Calanus finmarchicus	—	—	3	—	—	3	2	—	1	—	—	1	—	1	2
Temora longicornis	—	—	2	—	3	2	1	1	—	2	—	1	3	2	2
Other copepoda	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—
Total Copepoda	—	—	5	1	7	8	5	1	1	2	—	3	3	4	4
MYSIDACEA															
Leptomysis lingvura	—	—	1	3	1	5	2	14	26	66	87	2	2	24	22
Praunus flexuosus	—	—	—	2	1	1	1	2	1	—	—	—	1	—	1
Praunus inermis	—	—	—	8	1	—	—	—	1	—	—	—	—	—	—
Siriella jaltensis	—	2	3	3	3	1	1	2	1	3	9	1	—	2	1
Schistomysis spiritus	43	107	—	—	1	—	—	28	26	28	33	20	34	106	105
Other mysidacea	—	—	—	—	—	—	—	—	1	—	1	1	1	—	3
Total Mysidacea	43	109	4	16	7	7	4	46	56	97	130	24	38	132	132
ISOPODA															
Idotea baltica juv.	—	—	10	11	1	1	—	5	9	3	5	6	22	64	74
Other isopoda	—	—	—	1	2	7	2	—	—	—	—	—	—	—	1
Total Isopoda	—	—	10	12	3	8	2	5	9	3	5	6	22	64	75
DECAPODA															
Carcinus maenas megalopas	2	61	71	175	160	79	87	26	41	55	131	82	30	54	123
Spirontocaris sp. juv.	—	—	3	1	2	—	3	1	—	—	—	1	—	—	—
Crangon vulgaris juv.	—	—	—	—	4	1	—	1	1	—	—	—	1	6	3
Other decapoda	—	—	1	—	1	—	3	3	—	—	—	—	—	1	—
Total Decapoda	2	61	75	176	167	80	93	31	42	55	131	83	31	61	126
PYCNOGONIDA	—	—	—	1	1	5	1	8	4	3	—	1	—	4	—
POLYCHAETA															
Arenicola marina juv.	—	—	—	3	1	1	—	—	3	1	3	—	—	2	2
Other polychaeta	—	—	1	—	1	2	—	1	2	—	—	—	—	—	2
Total Polychaeta	—	—	1	3	2	3	—	1	5	1	3	—	—	2	4
OLIGOCHAETA	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Grand total	60	193	143	373	372	305	164	117	234	296	328	148	144	624	648

* Including 32 just-released juveniles.

mysis spiritus and two *Carcinus maenas* megalopas; by the second haul the two latter were much better represented, and had been joined by occasional individuals of several other species. To judge by the results of the day hauls (Table 1) there had probably been but little plankton over the beach before sunset, and these two night hauls probably show that *Schistomysis spiritus* and *Carcinus maenas* megalopas are the

first forms to migrate to the shore after sunset. It is noteworthy that the amphipod *Nototropis swammerdami*, which, lower down the beach and later at night, was sometimes the most abundant animal in the catches, only just made an appearance on 4 July, with three individuals in haul 2.

On 8 July five hauls were made on a rising tide, ranging from mean low-water springs to a little below high-water neaps. The lowest station was the first, and was probably taken too early in the night to catch more than the early arrivals. Nevertheless, this haul contained a large number of species, and the 8 July hauls as a whole contained more species than on any other occasion. On this night, in contrast to the others when it was calm, the sea was fairly rough (rough enough to make it difficult to stay upright while towing the net; the net itself was unaffected by the waves). Owing, perhaps, to the increased turbulence and water movement, several species occurred on this night only, or in greater numbers than on other occasions. These species included several which are truly planktonic, such as *Parathemisto oblivia*, *Anomalocera patersoni*, *Calanus finmarchicus* and perhaps the juvenile *Spirontocaris*. Perhaps this suggests that planktonic species actually avoid the sea's edge, unless forcibly carried there by wave action. *Carcinus maenas* megalopas, too, were on the whole more numerous on 8 July, but were also well represented on the other occasions, being indeed the most abundant species of all in seven out of the fifteen hauls. Other species which were more abundant on the rough night of 8 July included the amphipods *Apherus bispinosa*, *Gammarus locusta* (including *G. zaddachi oceanicus*), *Guernea coalita* and *Perioculodes longimanus*, and the Cumaceans *Bodotria scorpioides* and *Pseudocuma similis*. It seems that these species, though they may leave their daytime habitats at night, do not usually go very far, and may reach the shore only when carried there by wave action. It is possible that the young *Idotea baltica* (which will be considered again below) can to some extent be included in this category; although they were present in the first two (lowest) hauls, they seem to have prevented themselves being carried up the shore by the rising tide, and so to have avoided the surf zone during most of the night. These Idoteas, too, were more consistently present, and sometimes in much larger numbers, when conditions were calm. They have been examined by Dr E. Naylor, to whom we are most grateful. About a quarter were too young for determination, but of the rest all but two single specimens each of *I. granulosa* and *I. emarginata* proved to be *I. baltica*. The lines '*Idotea baltica* juv.' in Tables 5 and 6 include all these young stages.

In great contrast to the above group of species there are the two mysids *Leptomysis lingvura* and *Schistomysis spiritus*. These were the only mysids obtained by us in any quantity, but both were distinctly few on the rough night of 8 July. This was very marked in the case of *S. spiritus*; of the 531 caught, only a single individual appeared among the five catches on the night of 8 July. Now *S. spiritus* is one of the few species known to congregate along the water's edge in really large numbers; Liao (1951), for instance, on occasion caught as many as 250000 in a twelve minute haul with a D-net at Port Erin, a figure which might correspond with about 50000 in one of our hauls! We never caught mysids in anything like this abundance at Stoupe Beck, but nevertheless *S. spiritus* did usually appear in considerable numbers. Its occurrence in some quantity on 4 July, at the time of high water and very early in the night, may indicate

that some had been at the water's edge during the preceding afternoon and had been carried up the shore by the advancing tide. On calm nights, then, these mysids behaved to some extent as passive drifters at the water's edge; but on 8 July, when wave action was sufficient to force into the surf several species which normally tend to avoid it (and some of these species are good swimmers), *S. spiritus* and *Leptomysis lingvura* were able to take vigorous avoiding action and keep themselves out of the most troubled water.

The last two sets of hauls, on 10 and 12 July, illustrate some other aspects of the behaviour of this fauna. Both nights were calm, and those species, mentioned above, which seem to avoid the water's edge unless forcibly carried there, were present only in small numbers or not at all; the two sets of hauls differed, however, in that the set on 10 July started at about the time of low water and was continued on a rising tide, whereas on 12 July the tide was ebbing throughout.

Now the nearest likely home for some of these immigrant species is among the weed-covered rocks which lie off shore at a distance of some scores of yards from low-water mark; they must traverse this distance at least before they reach the water's edge. Few do so by day, as was shown by the daylight hauls on 26 June, when only the amphipod *Nototropis swammerdami* was caught in fairly large numbers, and of the minority which do swim as far as the water's edge by day, hardly any then continue with the advancing tide up the shore. Clark & Milne (1955) have shown that *N. swammerdami* may be abundant over the sand by day just below low-water mark. At night many more, both of individuals and of species, are to be found between tide-marks, though they do not reach the water's edge from their day-time haunts all at the same time. In the first hauls on 10 and 12 July, many of the species were present in much smaller numbers than they were later in the night; *N. swammerdami* and *Leptomysis lingvura* show this particularly well, and so does *Carcinus maenas* on 10 July. On this night the catches of these three species increased to the third haul, and to the fourth in the case of the latter two. *Nototropis swammerdami*, however, showed a marked decrease, from 112 to 37, between hauls 3 and 4; this, combined with its poor showings from the hauls highest up the shore (4 July, hauls 1 and 2, 8 July, haul 5), seems to indicate that although this species may be numerous at the water's edge when the tide is low, by day or by night, it does not follow the tide very far up the beach as a rule.

On 10 July, at any rate, the behaviour of *Schistomysis spiritus* was somewhat different; there were quite a number present (28) in the first haul, but the number did not increase to any extent in the later hauls. It looks as though those present at the water's edge at the beginning of the night remained there, and that any recruits coming towards the surf from farther out failed to move fast enough to catch it up as the tide rose. The young *Idotea baltica* may have behaved similarly. This idea gets some encouragement from the catches on 12 July, when the tide was falling. Again the first catch was a poor one and the second only somewhat better. But with the third and fourth catches there was quite a dramatic increase in the numbers of the commonest species, including this time both young Idoteas and *Schistomysis spiritus*. This makes it appear that the falling tide brings down with it the animals that have already invaded the shore, and that these are reinforced by the later arrivals, so causing a marked concentration of immigrants at low-water mark by midnight.

At this point it might be as well to summarize our conclusions about the general behaviour of these subtidal animals.

(1) It seems reasonable to suppose that, in calm weather at any rate, the water at the edge of the sea slides up and down the shore with the tide, and that it mixes relatively little with water more than a few feet deep.

(2) In rough weather there is enough turbulence and wave action to cause some mixing between the adjacent off-shore water and the surf.

(3) By day, most of the animals stay close to their homes in the seaweed-covered rocks and in the sand, some scores of yards below low-water mark; a certain amount of swimming goes on and a few species can be caught at the edge when the tide is lowest, but very few stay there to get carried up the beach.

(4) At night there is much more swimming, and many more individuals and species get as far as the water's edge and get carried up the shore. They do not reach the surf zone in any number until an hour or so after night-fall, and later immigrants continue to arrive during the night.

(5) In rough weather a number of species, including several members of the permanent plankton, appear between tide marks, where they have probably been forcibly carried by water-movements. But by way of contrast the two mysids *Leptomysis lingvura* and *Schistomysis spiritus* were conspicuously scarce on the rough night of 8 July, and can apparently in some way keep away from the surf zone when this is too turbulent; this is especially noteworthy in the case of *S. spiritus*, for this species is perhaps the most prone to seek the water's edge and stay there, as is shown by its occurrence in fair abundance early in the night in the two highest hauls, those of 4 July.

(6) It must be emphasized that the above conclusions are based on a limited number of hauls spread over only eight days, and are not necessarily applicable to other seasons. Fage (1933) showed that a number of species showed marked seasonal differences in their appearance in the night plankton.

These results from Stoupe Beck can be compared with work done on corresponding faunas elsewhere, notably by Tattersall (1911) at Clare Island, Fage (1933) at Banyuls and at Concarneau, and by Elmhirst at Millport (Elmhirst 1932; Watkin 1941). Fage made his collections by the light of a lamp, Tattersall by means of surface tow-nettings at night, both of them in shallow water immediately off shore but not in the surf zone. They caught large quantities of amphipods, and of the six most abundant species common to their lists four were among the most numerous in our hauls; these were *Nototropis swammerdami*, *Perioculodes longimanus*, *Guernea coalita* and *Apherusa bispinosa*. Moreover, the last three of these appeared in our catches in any number only on the rough night of 8 July. These facts, taken together, tend to confirm our suggestion made above that, although many subtidal species may spend some time in the plankton at night, only a few of them (such as *Nototropis swammerdami*) normally reach the water's edge, the others which may appear there having to be forcibly carried thither by wave action. Fage also showed that there are great seasonal variations in the specific make-up of this inshore fauna, which adds point to our remark that it would be inadvisable to generalize on our more limited data from Stoupe Beck.

Elmhirst made two main sets of hauls with a small plankton net at Kames Bay. The

first (Elmhirst 1932) consisted of two series in March and June, taken at three-hourly intervals at the water's edge, and simultaneously at the surface over the position of low-water springs and on the bottom at the two-fathom line. The second, which was later worked up by Watkin (1941), consisted of single hauls at the water's edge at regular intervals throughout the year, the hauls being of similar length (100 yd) to our own. This work provides a bridge between Tattersall's and Fage's collections and ours.

All four collections, in common with our own, are characterized by the presence of large numbers of a few species, accompanied by many species in one's and two's, and it is possible to make a quantitative comparison between those in Watkin (1941) and ours, since both lots were collected in much the same way. The order of abundance in the Stoupe Beck catches has been given in Table 3. The order at Kames Bay was very different, the catches being dominated by *Gammarus locusta* (3151), *Pseudocuma cercaria* (833), *Nototropis swammerdami* (530), *Idotea* sp. (177) and *Cumopsis goodsiri* (80). (The figures in brackets are the totals in forty-eight hauls. Beach crustacea have been omitted; they were much more numerous at Kames Bay than at Stoupe Beck (see Colman & Segrove 1955).) The chief differences are the abundance of *Gammarus* and cumaceans at Kames Bay (we only got thirty-eight *Gammarus* and forty-eight cumaceans altogether), and of mysids and of *Carcinus* zoeas at Stoupe Beck (Watkin recorded only occasional megalopas and zoeas). The prevalence of *Carcinus* megalopas at Stoupe Beck may be a seasonal phenomenon; at Port St Mary, Isle of Man, Southward (1953) recorded the continuous settlement of newly metamorphosed *Carcinus maenas* from June to October. The occurrence of *Gammarus locusta* at Kames Bay, however, was not seasonal, as they were present in greater or lesser numbers throughout the year (1936); they were absent from only eight of the forty-eight hauls, and these were made either in daylight or else high up the shore. It should be noted, however, that in his earlier collections Elmhirst (1932) found *Gammarus* more numerous than *Nototropis swammerdami* in March, and mostly at the edge of the tide, but that in June the picture resembled that at Stoupe Beck, with considerable, though reduced, numbers of *N. swammerdami*, but only a single specimen of *Gammarus locusta*. In a recent paper, Clark & Milne (1955) record the results of some trawling in shallow water at Kames Bay; the hauls were made in the winter and, apparently, by day. In the shallowest station, just below low-water mark, the catches were dominated by *Gammarus locusta*, *Nototropis swammerdami*, *Pontocrates arenarius* and *P. norvegicus*, and *Idotea baltica*, in that order. *Pseudocuma cercaria* and *Schistomysis spiritus* were also present in fair numbers. (They also record *Idotea viridis*, but this is not likely to be correct since this species is confined to brackish water (Naylor 1955*b*, Holthuis 1949).)

The abundance of cumaceans in the tidal plankton at Kames Bay and their fewness in that at Stoupe Beck seems to reflect their daytime abundance in the two localities. Watkin found them in some numbers in the intertidal sand up to above low-water neaps, whereas we did not. It is not profitable to compare the tidal plankton at Kames Bay and Stoupe Beck any further, until much more is known about the daytime population of sand, rocks and weed immediately off shore at Stoupe Beck. Almost or entirely absent from our plankton hauls were the intertidal rock-dwelling

amphipods such as *Amphithoë rubricata*, *Hyale nilssoni*, *Marinogammarus obtusatus* and *Melita palmata*; our hauls all ended up within about 50 or 70 yd of an extensive, weed-covered reef where these species are abundant. From this it would seem that the intertidal rock-dwellers, like the intertidal sand-dwellers, do not make the extensive horizontal excursions characteristic of some of their subtidal neighbours.

(*c*) *Vertical distribution*

In the preceding section, each haul has been treated as a unit, the catches of the top and bottom nets having been added together in each case. If now the top and bottom nets are treated separately, some information can be derived about the vertical distribution of the fauna, since the bottom net sampled from 2 to 8 in., and the top net from 8 to 14 in. above the sand. It might be expected that in the surf zone there would be sufficient turbulence, particularly on the rough night of 8 July, to keep the water so stirred up as to make the catches of the two nets roughly the same. Quite definitely, however, this was not the case. Most of the species occurred in numbers too small to permit of analysis in this way, but the vertical distribution of the twelve most abundant species is shown in Table 6, in which the hauls are arranged in chronological order, as in Table 5. The species fall into three remarkably distinct groups: (1) little or no difference between top and bottom nets; (2) about twice as many in the bottom net as in the top net; (3) about twice as many in the top net as in the bottom net. There is no overlap between the groups, though if more species had been available it is possible that the picture would have been less clear-cut.

The first group, where the animals are evenly distributed between the two nets, consists of three subtidal amphipods, *Apherusa bispinosa*, *Gammarellus homari* and *Nototropis swammerdami*. Sometimes the top net contained more, sometimes the bottom, and this may indicate a certain patchiness in the distribution, but the totals for the two nets are very similar and show that these species are fairly evenly distributed in the surf zone, and show no preference for or avoidance of the bottom or the surface. This should not be taken as necessarily indicating the behaviour of these species in somewhat deeper water; Elmhirst (1932) found that in two fathoms *N. swammerdami* was more numerous near the bottom than at the surface.

The second group, where there were at least twice as many in the bottom net as in the top, includes animals of two quite distinct ecological habits. On the one hand there are the intertidal forms *Bathyporeia sarsi*, *B. pelagica*, *Pontocrates norvegicus* and *P. arenarius*; their distribution in the two nets confirms our conclusions (see p. 453) that their swimming excursions are of short duration, and shows that as a rule they do not get more than a few inches off the bottom. On the other hand, there are the young *Idotea baltica* and the two mysids *Schistomysis spiritus* and *Leptomysis lingvura*. These are all detritus feeders, at any rate for part of the time (Naylor 1955*a* and personal communication, Cannon & Manton 1927), and their concentration near the bottom perhaps reflects their feeding habits.

The third group, where the catches in the top net were twice as great as in the bottom net, includes the cumaceans and the megalopas of *Carcinus maenas*. It seems unexpected that the cumaceans should belong to this group and the mysids to group 2,

Table 6. *Night hauls in July 1949; vertical distribution*

The catches in the top and bottom nets of the plankton trawl are shown for 12 species, figures for the bottom net in italics.

	4 July		8 July					10 July				12 July				
Haul no.	1	2	1	2	3	4	5	1	2	3	4	1	2	3	4	Total
GROUP 1: similar numbers in top and bottom nets																
Apherusa bispinosa	—	—	—	14	12	3	—	—	1	3	1	1	—	2	—	37
	—	—	*2*	*13*	*4*	*2*	—	*1*	*1*	*1*	—	—	*3*	*2*	*2*	*31*
Gammarellus homari	—	—	—	8	—	—	—	—	3	3	2	—	2	9	5	32
	—	—	—	*3*	*1*	—	—	*1*	—	*7*	—	—	*3*	*8**	*6*	*29*
Nototropis swammerdami	—	1	9	31	13	20	4	2	50	29	21	1	15	142	127	465
	—	*2*	*16*	*27*	*5*	*17*	—	*7*	*42*	*83*	*16*	*1*	*13*	*117*	*117*	*463*
GROUP 2: more in bottom than in top net																
Bathyporeia sarsi	—	1	—	—	4	6	3	—	2	—	—	—	—	—	—	16
	—	*1*	—	—	*8*	*9*	*1*	—	—	—	*3*	—	—	—	—	*23*
B. pelagica	—	—	—	3	6	4	1	1	—	1	1	—	—	—	1	18
	—	—	*1*	*5*	*3*	*32*	—	*1*	—	*1*	*6*	*1*	—	*2*	—	*52*
Pontocrates norvegicus	—	—	—	8	21	26	4	1	1	1	3	8	6	—	1	80
	14	*27*	*2*	*9*	*44*	*36*	*9*	*1*	*1*	*1*	*3*	*16*	*2*	*2*	*2*	*159*
P. arenarius	—	—	—	—	—	—	—	—	—	—	—	—	—	2	9	11
	—	—	—	—	—	—	—	*2*	*6*	*2*	—	—	—	*5*	*19*	*34*
Idotea baltica juv.	—	—	4	5	1	—	—	1	4	1	2	1	4	17	25	65
	—	—	*6*	*7*	—	*1*	—	*4*	*5*	*2*	*3*	*5*	*18*	*47*	*50*	*148*
Schistomysis spiritus	1	27	—	—	1	—	—	2	9	6	13	5	14	37	36	151
	42	*80*	—	—	—	—	—	*26*	*17*	*22*	*20*	*15*	*20*	*69*	*69*	*380*
Leptomysis lingvura	—	—	—	2	—	2	1	2	7	11	23	2	—	6	12	68
	—	—	*1*	*1*	*1*	*3*	*1*	*12*	*19*	*55*	*64*	—	*2*	*18*	*10*	*187*
GROUP 3: more in top than in bottom net																
Bodotria scorpioides	—	—	2	3	4	1	6	1	—	1	—	—	—	2	1	21
	—	—	*1*	—	*1*	*1*	*4*	*2*	—	—	—	—	*1*	—	—	*10*
Carcinus maenas	—	48	35	132	88	47	64	8	29	50	98	28	20	42	104	793
megalopas	*2*	*13*	*36*	*43*	*72*	*32*	*23*	*18*	*12*	*5*	*33*	*54*	*10*	*12*	*19*	*384*

* Excluding 32 just-released juveniles.

when the former are, by day, even more bottom-loving than the latter, and when the feeding habits of both groups are not very dissimilar (Fage 1951). In all but four hauls the megalopas were more numerous in the top net, and it is curious that the exceptions should be the first hauls on each of the four nights, all taken within an hour or so of sunset. It would be tempting to argue from this that the megalopas had avoided the plankton by day, and were still only emerging and still taking up their night-time positions near the surface when these early hauls were taken, but this is opposed by the fact that these larvae were among the few animals present at all levels on the shore in the daytime hauls (see Table 1). Perhaps the most surprising thing is the way in which both cumaceans and megalopas were able to maintain this pronounced vertical distribution on the night of 8 July, when there was quite a sea running and turbulence was considerable at the level where the net was being towed. This calls for remarkable powers of swimming and of orientation on the part of these animals.

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SUMMARY

1. Five series of hauls (one by day and four by night) were made with a special bottom plankton trawl, which is described in detail, over Stoupe Beck Sands, Robin Hood's Bay, in June and July 1949; the hauls were made in 2 ft of water at the edge of the tide at various levels on the shore.

2. The day-time catches were very poor, with the exception of the first which was taken below low-water mark; this first catch was not inferior to some of those made by night.

3. The night catches contained both intertidal, sand-inhabiting amphipods and also immigrants whose daytime habitats lie well below tide marks.

4. The appearance of the sand-inhabiting forms corresponded very closely to their zonation on the beach; they were more numerous near the bottom of the water than at the surface, and only a very small proportion of those known to be present were in the plankton.

5. The immigrant forms were dominated by amphipods, mysids and *Carcinus maenas* megalopas, the various species reaching the edge of the tide successively. In rough conditions the two commonest mysids avoided the surf, while other species, including members of the permanent plankton, were brought in, presumably in horizontal water-movements caused by turbulence. The factors influencing this fauna are discussed.

6. The immigrant amphipods showed a roughly even vertical distribution; the mysids were twice as numerous towards the bottom, whereas the crab megalopas and cumaceans were twice as numerous towards the surface, in 2 ft of water.

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REVIEWS

POPULATIONS IN THEORY AND EXPERIMENT

A. J. Nicholson (1954). Experimental demonstrations of balance in populations. *Nature, Lond.* **173**, 862.

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These three papers deal with population dynamics in cultures of blowflies, but the greater part of the last one sets out a deductive theory of population regulation which can be considered separately. It is put forward as a framework for experimental and theoretical work to be published later. There is little reviewing of recent literature, and references are given chiefly on points of disagreement. While Dr Nicholson's views remain fundamentally the same as in his earlier works, here they are thought out afresh and re-stated in more easily readable terms. His present preoccupation with competition in populations of blowflies rather than with insect parasites has led to various changes of emphasis and some new developments.

Briefly, the theory holds that populations regulate their own densities, by depleting or impairing essential supplies, or by maintaining enemies; the usual mechanism is intraspecific competition, either among the animals or among their enemies. These processes hold populations in a state of moving balance. The effect of a destructive factor tends to be reduced by compensatory reaction. The factors which (through competition) regulate populations are density-dependent, but density-independent factors may greatly influence the level of density about which the numbers are regulated. The density-dependent action of regulating factors arises from the limited supply of various requisites, notably food. Nicholson defines four types of reaction to these factors and three types of requisites. By combining them he derives eleven patterns of population growth and maintenance, including a number of differently shaped curves of oscillation. Oscillations and fluctuations of populations in a community tend to interfere with one another, giving rise to irregularities with no evident relation to external changes. Further irregularities arise from the fact that populations are often scattered as more or less isolated groups in various stages of increase or decrease.

Nicholson recognizes the importance of the non-regulatory factors, especially physical conditions, in 'setting the scene' for the action of the regulatory ones, indeed in determining which of several regulators shall be the dominant one at a particular time, as well as in modifying its action to an extent which greatly influences the level of density.

It can be objected that populations are not necessarily under continuous regulation by density-dependent influences. Some insects, for example, seem to spend most of the time recovering, by annual increases, from occasional climatic setbacks; density-related influences may play an important part only in the event of very high density being reached before the next cataclysm, or at the stage of low density following it, when a concentration of natural enemies may impose a severe reduction of the survivors. Such populations are at most times not being regulated, in the sense of being controlled by density-related processes; they are increasing, decreasing or fluctuating chiefly according to the physical conditions and sometimes the state of their food, within limits of density where (at least for the time) the density-related regulatory processes have little effect. All that Nicholson concedes in this direction is that if environmental conditions are unfavourable at times, 'density governance is merely relaxed from time to time and subsequently resumed, and it remains the influence which adjusts population densities in relation to environmental favourability'. But often the physical conditions become unfavourable again before the numbers are high enough to occasion density effects. On the other hand, to expect this state of affairs to continue indefinitely is to ask too much of pure chance, and the above reservations do not excuse us from seeking the mechanism of long-term regulation.

It is sometimes objected that many populations are limited simply by the supply of one or more requisites such as food, nesting-sites, etc., and that in such cases the idea of density-dependence is superfluous. This is like saying that the volume of a confined gas is determined by the size of the containing vessel, and that we need not consider the pressure of the walls upon the gas. In each case the first part of the statement may be perfectly true, but we cannot escape the second consideration if we wish to bring these specific cases into line with others, and to make generalizations about the limitation of populations or what determines the volumes of gases.

While the idea of density-dependence is basic to Nicholson's theory, the term has been rather inconsistently used, and he introduces a new terminology for the purposes of his argument. This may give rise to a preliminary despondency in the reader, but in fact the terms are clearly defined and mostly well-chosen, and do serve to clarify the discussion.

The author raises many interesting and controversial points which cannot be taken up here. One that should provoke experiment as well as thought is his comment on the famous cultures of Protozoon predators and prey in which Gause failed to reproduce the periodic oscillations predicted in the mathematical theory of Lotka and Volterra. Nicholson suggests that Gause's experiments were conducted with too few organisms in too small a space, and that this was the reason why his *Didinium* destroyed all the *Paramecium* at an early stage instead of showing oscillatory interactions like those in his cultures of *Paramecium* and yeast.

The other part of the work under review is a brief account of experiments with laboratory cultures of an Australian sheep blowfly, *Lucilia cuprina*. Most experiments ran for about a year, in a battery of large cages, under closely controlled conditions. The adults were provided with ground liver, sugar and water, the larvae with meat. The population could be limited by restricting the supply of one or more of these requisites.

In some experiments the supply of protein food for the adult flies was restricted. The resultant competition, with a lot of wastage at high densities, led to an inverse relation between the numbers of flies and the numbers of eggs laid; but owing to the time lag between the laying of the eggs and the emergence of the resulting adults, the flies alternately far overshot and undershot the equilibrium level. Thus, when there were many adults, competition for the food was so severe that few eggs were laid, so the adult population was not replenished, and fell to a low level; this reduced competition, many eggs were laid, and the population of adults again rose too high.

In other experiments the population was limited by restriction of the larval food; when severe competition eliminated most of the maggots, there were relatively few flies and eggs produced, and larval competition in due course slackened off, so allowing another wave of overpopulation. In certain experiments of this type, a high percentage of the emerging adults were artificially eliminated. This alleviated competition, whether for adult or for larval food, and so (in conjunction with other effects of a similar kind) allowed an increase in the population. So the imposed destruction evoked a compensatory increase, which passed through the life cycle up to the stage of destruction. Because of these compensatory processes, populations were not reduced in proportion to the imposed destruction, and in some circumstances were even increased by it.

Because competition in *Lucilia* is so keen and so wasteful, these experiments provide excellent examples of some of the processes of competition, compensation and regulation in their elemental forms. If many field populations showed such clear and simple relationships, Nicholson's theory might be accepted by all ecologists. However, as he admits in parts of the discussion, the state of affairs under field conditions is generally much more complicated and difficult to analyse. (In certain passages he seems to underestimate this important difference.) Indeed, many ecologists doubt whether the distinction between density-related regulating processes and modifying processes can be maintained in practice, and some conclude that climatic and other influences acting in ways not significantly related to density can maintain natural control. Others are more impressed by those cases in which density-related controls, such as insect parasites, are known to keep populations in check, and by the logical necessity of relating density-regulation to density. Some day, perhaps, when the logic has been developed in more concrete terms by application to varied field studies, and when some of the examples which seem to resist the logic have been more fully analysed, the yawning gap will close, and the protagonists will incredulously find themselves standing on common ground. Or perhaps not.

M. E. SOLOMON

THE ECOLOGY OF POPULATIONS

H. G. Andrewartha and L. C. Birch (1954). *The Distribution and Abundance of Animals.* Pp. xvi + 782; 214 text-figures. Chicago: University of Chicago Press; London: Cambridge University Press. Price £5 12*s.* 6*d.*

This large book is essentially within certain limitations of definition a text-book of animal ecology. It deals mainly with terrestrial animals and more with invertebrates, especially insects, than with vertebrates. There is very little on soil animals. In their first few pages the authors decide that the study of whole communities of animals is scarcely possible and only doubtfully useful. They therefore attempt to construct a general theory of the determination of the distribution and abundance of animal species, one at a time, the other animals and plants being considered as part of the environment. Even those who do not agree with this way of treating ecology will find that many problems of interest to all ecologists are discussed in an admirably logical way and with great lucidity. Many points which have previously been overlooked or whose treatment has been muddled or obscure are here clearly set out and fully explained. The analysis of the meaning of the word environment and the discussion of the logistic curve may be mentioned as examples. An especially valuable feature of the book is the large number of examples taken from the more recent zoological literature; these are often excellent summaries of a series of papers. The system of numbering chapters, paragraphs and examples by means of a decimal notation makes for clarity and great ease of cross reference though the application of the same system to the numbering of the illustrations is at first a little confusing.

The subject-matter of the book may be very briefly summarized as follows. After two introductory chapters, the next three deal with certain innate properties of species which are found to be of special ecological importance. These are the capacity for increase in numbers, the phenomena of diapause (chiefly of importance in insects by determining the frequency of generations), and data concerning natural dispersal. The discussion of the innate capacity for increase is a valuable exposition of methods which are becoming of considerable importance in ecology, especially in studies of vertebrates. I think, however, it is easy to exaggerate the value of life-tables constructed in the laboratory. While one may be able to control the environment, particularly such features as temperature and humidity, it is impossible to allow for the effects of the particular methods of culture which are equally relevant.

Chapters 6–12 constitute an analysis of the environment under the following headings: weather (temperature, moisture, light), other animals of the same kind, other organisms of different kinds, food, and a place to live. The conclusions and theories derived from this material are tested out on a number of well-studied natural populations in chapter 13. The whole of this chapter is of exceptional interest. A rather brief fourteenth chapter summarizes the authors' views on what does in fact determine the density of natural populations. The last two chapters deal with genetics and the origin of species in relation to ecology. They include information which has been discussed more fully elsewhere and might perhaps have been omitted without much harm to the book. Now that geneticists themselves undertake ecological studies there is less need for ecologists to blow this particular trumpet.

In spite of the considerable number of examples which are quoted from field studies of natural populations the book must, I think, be regarded as theoretical rather than practical. No doubt this was the deliberate intention of the authors but it has perhaps been carried too far. A great deal of the difficulty of animal ecology is to find reliable ways of doing what most ecologists think ought to be done. Methods therefore are still of great importance. Examples of the over-theoretical cast of the book are the following. A section called 'methods of sampling' occupies less than one page (p. 558). The discussion of tests for randomness of distribution which follows is quite inadequate, the whole concept of randomness in natural populations requiring clearer definition and much more study. If a significant feature of the environment (e.g. a relatively rare food-plant) is distributed at random, an animal attached to it may also be distributed at random in a purely spatial sense, i.e. as measured by co-ordinates from two arbitrary base-lines. But when we say that species are distributed at random do we often mean much more than that we do not know the causes of their distribution? The subject is far from an academic one, for the appropriate tests of significance for population estimates may depend on the type of distribution of the population. There has been too great a tendency to assume

that methods devised for agricultural plots will be equally suitable to the more complex natural distributions.

The most controversial part of the book is the discussion scattered through it of the importance of competition and of density-dependent factors. Most discussions of these points both here and by other authors have unfortunately become infused with emotions which are easily discernible through the façade of cold rationality. It is unlikely that my own view is more unbiased than that of anyone else, but it has always seemed to me intuitively obvious that any organism increasing geometrically as all living organisms normally do can only be kept in ultimate check by a mortality which is dependent on the density of the species. This seems to be quite independent of any particular mathematical theory and is not disproved by showing that some particular mathematical model is in some respects incorrect or unlifelike. The authors are probably right in suggesting that the importance of predators and parasites as density-dependent factors has been exaggerated. It is all the more necessary to discover how climatic factors may themselves come to act in this way. It is possible that a more detailed study than that of chapter 5 of natural dispersal and of the behaviour and physiological changes which lead to it might be helpful here. I believe the authors are also right in following W. R. Thompson and focusing attention on the patchy nature of the environment, both in space and (as regards weather) in time. This is undoubtedly a great complication in any simple exposition of how natural populations are likely to be controlled but I fail to see how it can be made a substitute for the periodic intervention of density-dependent factors. This part of the subject seems to me to need much more consideration; it is perhaps uncertain how far it is legitimate to apply general theories to small segments of the whole population of a species. The second law of thermodynamics which occupies a somewhat analogous position in physics does not necessarily apply to small subsystems (e.g. single animals) which are arbitrarily but not physically isolated from the whole system.

The authors' treatment of periodic variations in the numbers of animals raises a somewhat similar difficulty. It seems, at least to me, intuitively obvious that the interaction between a host and its predator will give rise to periodic fluctuations in their numbers and that the bigger the complex of species involved the more likely to be damped are the amplitudes of the fluctuations. This again seems to be quite independent of any particular mathematical model. It might perhaps be said that the authors use rather a lot of space in trying to disprove what they disbelieve; one would like to see something more substantial substituted for what is removed.

These criticisms do not reduce the value of a large part of the contents, and even if the authors' views are in some respects incorrect I think they will have done a great service in forcing everyone to think more carefully.

The work concludes with a long and useful bibliography and a full index. It is very well produced and only a very few misprints have been noticed. O. W. RICHARDS

GENETICS AND ECOLOGY

I. Michael Lerner (1954). *Genetic Homeostasis.* Pp. vii + 134. Edinburgh: Oliver and Boyd. Price. 12*s.* 6*d.*

A welcome trend in post-war biological research has been an ever-growing convergence of views among ecologists and geneticists. This has already paid valuable dividends, particularly in the experimental study of evolution. Unfortunately, the diversity of the literature on both sides of the Atlantic makes ecological genetics a difficult subject to study, and any attempt at a synthesis of even a small part of this field is therefore most welcome.

Professor Lerner's book is concerned with a vital and fundamental attribute of all living organisms, namely their ability to maintain a constancy of internal environment (homeostasis) in the face of fluctuating external conditions. The capacity of an animal or plant for maintaining such internal stability must inevitably determine its ability to become adjusted to a changing environment and, hence, its potentiality for evolution. As the author points out, isolated populations must always possess certain self-regulating properties enabling them to achieve a maximum average fitness in the particular circumstances in which they happen to exist. In this respect it seems likely that heterozygotes would be at an advantage over homozygotes in promoting self-regulation (genetic homeostasis) since natural selection will tend to favour intermediate rather than extreme phenotypes.

From the ecological viewpoint concepts such as these raise many problems of great interest and importance in wild populations. Unfortunately, the whole of this book is heavily weighted towards the genetic side and is concerned almost entirely with the results of domestication and laboratory breeding. As such it will be of relatively little value in initiating the ecologist into the more genetical approach, although it will undoubtedly be useful to the geneticist.

These limitations obviously arise from the fact that, as Professor Lerner says, he is a student of animal improvement, rather than a naturalist. In spite of this, it seems rather remarkable that he should not even mention some of the classical work now being carried out in his own field on wild populations both in Britain and in the United States. The extensive studies of Ford and Sheppard at Oxford on *Panaxia dominula*, to quote a single instance, find no place, even in the bibliography. The book would be improved by the addition of an index.

W. H. DOWDESWELL

DESERTS

J. L. Cloudsley-Thompson (editor) (**1954**). *Biology of Deserts. The Proceedings of a Symposium on the Biology of Hot and Cold Deserts organised by the Institute of Biology*. Pp. ix + 224. Published by the Institute of Biology, London.

The accommodating word 'biology' is here used to cover a symposium of 28 papers which range over a very wide field, from the causes of deserts and the physiology of their fauna and flora, to the microbiological formation of sulphur in lakes and the irrigation schemes of the U.S.S.R. Despite the subtitle, it is the hot-and-cold arid deserts and semi-deserts, particularly of Africa, the Near East and Australia, that almost all the speakers have in mind and not the true cold deserts of mountains and the polar regions.

Several speakers deal with the physical conditions of arid deserts, naturally laying particular stress on the occurrence of water: subterranean, when it may be too salt for plants or even animals; seasonal; or sporadic, when a measure of the number of years between rain is often more pertinent than annual rainfall. But to a biologist it is the adaptations of animals and plants to these severe conditions that are likely to be of particular interest, an interest associated by most zoologists with Buxton's well-known book. The locust, like the Arab, is nomadic and there is some evidence that its flights may be directed towards areas where rain is likely and conditions may become suitable for reproduction. Small mammals are partially subterranean and make extensive use of metabolic water. Fur becomes an important insulator against external heat and larger animals have the advantage over smaller ones that they can lose more heat by evaporation for a particular percentage loss of water. Where there are seasonal climatic changes it is only to be expected that animals and plants exhibit seasonal rhythms.

About half the papers deal with the cultivation of deserts and a number of interesting problems are discussed. They fall, however, into familiar categories: the need for careful management to avoid overworking; the menace of the introduced pest and the new pest arising from indigenous populations; and the difficulty of finding suitable human labour. In a biological symposium it is as it should be that two or three speakers consider how local crops and herds can be managed to man's best advantage, rather than how environment, crops and herds can all be changed.

The book has been produced by a method which leaves a ragged right-hand margin and gives the page a type-written look. If it is by such techniques that the rises in publication costs are going to be offset then we must hope that they will in time achieve the same high standards that we have become accustomed to in books produced by more conventional methods.

D. A. PARRY

P. A. Buxton (**1923**, reprinted **1955**). *Animal Life in Deserts*. Pp. xvi + 176; 43 text-figures and photographs. London: Arnold. Price 21*s*.

Dipping again into this well-known book one is surprised to find that it was first published as long ago as 1923, so fresh is its style and outlook. The publishers write of 'many demands for its reissue'; it is satisfactory that it should be again available to new generations of ecologists.

OCEANIC ENTOMOLOGY

J. L. Gressitt (1954). *Insects of Micronesia.* Vol. I. *Introduction.* Pp. ix+257; 70 maps and photographs. Honolulu: Bishop Museum. (No price given.)

Much of the material which will form the basis of the *Insects of Micronesia* which has been undertaken by the Bishop Museum of Honolulu, has already been collected. Publication will involve a long series of technical papers by numerous specialists. It is intended that eventually a summary shall be published dealing particularly with zoogeography and the development of species in small isolated islands. Here we have the Introduction to the work written by Dr Gressitt, entomologist of the Bishop Museum.

Micronesia, in the sense used here, includes five principal island groups, the Gilberts (but not the Ellice Islands), the Marshalls, Carolines, Marianas and Bonin Islands. It extends from just south of the Equator to nearly 30° N., i.e. to well outside the northern tropic and over about 50 degrees of longitude. It is an immense area of ocean with a very small proportion of land in it, but an enormous number of individual islands.

In this vast area the geologist will find two main types of islands, the high volcanic ones and the low coral islands or atolls. There is an interesting contrast, not only in the physical types and the soils, but also in the antiquity of the two types of island, for it is held that the high islands are at least a thousand times as old as the atolls. Several factors therefore contribute, it would seem, to the poverty of the flora and fauna of the atolls.

Gressitt's introductory account is written on a wide base. He points out that the native peoples of Micronesia are very different from one another but that they may all be regarded as coming from south-east Asia or Indonesia. He includes a consideration of the effect of human beings in distributing useful or cultivated plants and therefore insects: the position has been complicated by the movements of men of European and of Japanese stock who have introduced new crops, new types of agriculture and also fast transport. It would, we feel, have been welcome if more attention had been given to the ethno-botany, as it is sometimes called, of the native Micronesians: we should like to hear of the interesting contrast which prevails between insects which are dependent upon the old food and other economic crops of the natives and those foreign insects attached to the new crops which have come in during the nineteenth or twentieth century.

As to the insects, it is to be understood that none of the technical papers is yet available, so that the entomological section is brief and confined to a history of expeditions with names of collectors in different island groups. The author has wisely avoided making even a brief statement about affinities between different island faunas, degree of similarity and so forth. The total amount of material now available for study is so much greater than what has been collected before that any such account would be scarcely justifiable. It is, however, made clear that the insect faunas are essentially 'oceanic'.

The existence of an Introduction such as this, published while the specialists are still working on the material will be of great value to them. It will have a tendency to give a common point of view as well as a fund of fact, and we see a considerable gain in that. P. A. BUXTON

VERTEBRATE ECOLOGY

G. A. Novikov (1953). *Polevye issledobaniya po ekologii nazemnykh pozvonochnykh* (*Field investigations on the ecology of terrestrial vertebrates*). Pp. 502. (2nd ed.) Moscow. Price 11 r. 90 kop.

This book, 'published by the Ministry of Higher Education as a text-book for State Universities', gives an interesting picture of the present state of ecological studies in the Soviet Union and it is also a useful source of references to a great deal of Russian work on ecology and natural history whose published results are not easily accessible in this country. It seems to be designed primarily as a hand-book for collectors and field ecologists rather than as a text-book for students and, as a useful compilation of miscellaneous information, it would be worth its place in the equipment of any field expedition. The emphasis throughout is on the importance

of field studies, and the zoologist is advised to get out of the laboratory into forest, tundra and desert to study Nature under genuinely wild conditions.

The first 170 pages are concerned with the planning, organization and equipment of expeditions, with methods of observing and capturing wild animals, of preparing and labelling specimens, of making field sketches and faunistic maps, and so on. There are illustrated instructions for preparing skins of mammals and birds, illustrations of conventional signs for different species to be used on sketch maps, reminiscent of military map-marking systems, and pictures of a dozen different traps for mammals. These last are all of familiar types, apart from a contraption for catching moles looking less effective than the ordinary English mole trap, which is not described. In this section there is a wealth of not particularly new information which it is convenient to have together in one volume, and it is not easy to think of a single up-to-date book in English in which it could all be found.

There is then a long chapter on the quantitative estimation of populations of various animal species, using simple methods of sampling small areas or of counting birds seen on a transect. There is no mention of capture-recapture methods, nor of pre-baiting traps, nor is there any discussion of statistical methods. The omission of the latter, however, is deliberate and the student is referred to several books which are said to deal fully with both Russian and foreign work on the subject.

Investigations of the ecology and habitats of mammals and birds are dealt with in the next two chapters. Subjects discussed include the study of food collection by great tits using artificial nestlings, changes in the bird population of woods according to the age of the trees, and seasonal or diurnal changes in the behaviour of birds and other vertebrates. There is a section on the dynamics of population growth, cyclical changes in numbers being mentioned briefly, with references to other published work. Finally, there is a chapter on techniques for investigating the micro-climate, with illustrations of some of the simplest forms of apparatus suitable for use in the field. Throughout the book numerous examples are given of the use of the methods described as applied to specific animals and problems. From the point of view of the foreigner it is a pity that only the vernacular names of species are used, although in the section on labelling specimens the importance of including the Latin name is emphasized.

For foreign readers the bibliography is perhaps the most useful part of the book. It gives over 800 references, two-thirds of them since 1945, classified according to subject in 31 sections; the section on the quantitative estimation of mammals, for instance, has 118 entries, and that on the feeding habits of birds, 32. So far as can be seen there are no references at all to non-Russian work.

Paper and binding are well below the standards we are accustomed to in this country. So also is the price; with 502 pages $8\frac{1}{2} \times 5\frac{1}{2}$ in. and 127 line illustrations the book sells in England at 10*s*.

C. B. GOODHART

François Bourlière (1955). *The Natural History of Mammals*, translated from the French by H. M. Parshley. Pp. xxii + 363 + xi; 24 plates; 97 text-figures. London: Harrap. Price 21*s*.

Our knowledge of mammalian ecology and ethology has been greatly augmented during the past quarter of a century by a number of field mammalogists (to use the convenient, but etymologically regrettable, American term). Unfortunately, as Dr Bourlière points out, their results have mostly been published in specialist journals difficult of access, with the consequence that it is not uncommon even to-day to see articles on mammals 'which, from the ethological and ecological point of view, could have been written half a century ago'. The lack of any broad survey of the existing state of our knowledge is now largely rectified by the present volume, and students of mammals owe a considerable debt to the author for having filled the gap so well. Dr Harrison Matthews's book on *British Mammals* in the New Naturalist Series, published in 1952, has brought together a great deal of what is known on the British species, and the present work covering mammals in general will be most useful at a time when the growing popular interest in mammals is evidenced, for example, by the recent formation of the Mammal Society of the British Isles.

The themes of the ten chapters are Locomotion; Feeding Habits; Home, Territory and Home Range; Defence and Protection; Sexual life and Reproduction; Development and

Longevity; Migrations; Social Life; Mammals and Their Environment; and the Structure and Dynamics of Natural Populations. The interrelations between these different aspects of mammalian life may be illustrated by the following passage: 'The sedentary nature of many small mammals, further, has consequences that would have hardly been suspected before the intensive studies of the last few years. Howard, having marked 675 young deer mice before they left the nest, found that 70 per cent of the young males and 85 per cent of the young females settled down no more than 500 feet from their birthplace. A high degree of inter-breeding results from this; 4 to 10 per cent of the 186 litters observed were produced either by parent-offspring matings or by matings between sibs.' It may be noted by way of contrast that the family range of wolves, studied by Murie in Mount McKinley National Park, may have a diameter of 50 miles.

Though the author has limited himself to the chief problems and various aspects are therefore left untouched, one feels that in a work on the comparative habits of mammals and their relations to their environment some account of the senses of mammals would have been welcome. Such words as sight or vision, hearing, olfaction, etc., do not appear in the index, and a search for any reference to what is known about colour-vision or the lack of it in mammals gave no result. Henderson and Craig's *Economic Mammalogy*, admittedly a compilation but one containing numerous facts relevant to topics here discussed, could with advantage have been included in the bibliography. The author's acceptance of the existence of true migrations in the American bison when it was abundant is at variance with the latest and most comprehensive monograph on the species (that of Roe). And in the Table of potential longevities, based mainly on Blower, the maximum for the grey seal is still given as 18 years, though Dr Erna Mohr and the present reviewer have both published authenticated cases of specimens twice that age or more. These are minor points, and the book with its extensive bibliographies is likely to prove an invaluable source of reference for a long time to come.

The translation, which reads like an original, was done by the late Professor Parshley, who also worked out with the author the numerous additions and revisions made to the French work, *Vie et Mœurs des Mammifères*. The photographs are not only of a high standard technically but have been carefully chosen to depict a wide variety of important and seldom-illustrated aspects of mammalian life; while the skilful and attractive text-drawings by Paul Barruel, whose abilities as naturalist and artist will be familiar to many from his *Birds of the World* and other works, have, in the author's words, freed the text from much arid descriptive matter.

COLIN MATHESON

James Fisher (1954). *Birds as Animals.* I. *A History of Birds.* Pp. x + 205; two text-figures. London: Hutchinson's University Library. Price 8*s.* 6*d.*

This is the first part of a greatly extended re-issue of the author's book *Birds as Animals* first published in 1939. It deals with the history of ornithology, distribution, systematics and bird populations. It contains an immense number of facts about birds: so great a number, indeed, that the reviewer found it almost impossible to see the wood of ornithology for the density of the trees! The compression of so much material into a small compass does not make for easy reading, and this is to be the more regretted in that many of the facts presented are not readily accessible to the non-specialist reader.

P. H. T. HARTLEY

BOOKS RECEIVED

Elements of Ecology. By GEORGE L. CLARKE. New York: Wiley; London: Chapman and Hall. 1954. Price 60*s*.

The Western End of Lake Erie and its Ecology. By THOMAS H. LANGLOIS. Ann Arbor, Mich.: Edwards. 1954. (No price given.)

Walt Disney's 'Living Desert'. By JANE WERNER and the staff of the Walt Disney Studio. London: Adprint. 1954. Price 8*s*. 6*d*.

North American Moose. By RANDOLPH L. PETERSON. Toronto University Press; London: Cumberlege. 1955. Price £5.

The Nuffield Foundation: Ninth Report. Oxford. 1954.

Studies of the Psychology and Behaviour of Captive Animals in Zoos and Circuses. By H. HEDIGER, translated by GEOFFREY SIRCOM. London: Butterworth. 1955. Price 30*s*.

The Biology of a Marine Copepod, Calanus finmarchicus *Gunnerus*. By S. M. MARSHALL and A. P. ORR. Edinburgh: Oliver and Boyd. 1955. Price 21*s*.

Bird Navigation. By G. V. T. MATTHEWS. Cambridge University Press. 1955. Price 12*s*. 6*d*.

The Origin of Vertebrates. By N. J. BERRIL. Oxford: Clarendon Press. 1955. Price 25*s*.

The Natural History of Tsetse Flies. By P. A. BUXTON. London: Lewis (London School of Hygiene and Tropical Medicine Memoir, no. 10). 1955. Price £4. 4*s*.

Die Binnengewässer in Natur und Kultur. By A. THIENEMANN. Berlin: Springer. 1955. Price DM. 7.80.

Précis d'Écologie animale. By F. S. BODENHEIMER, translated by J. THEODORIDES. Paris: Payot. 1955. Price 1200 fr.

Bird Recognition: 3. By JAMES FISHER. Harmondsworth: Penguin Books. Price 3*s*. 6*d*.

Microbes and Us. By HUGH NICOL. Harmondsworth: Penguin Books. 1955. Price 2*s*. 6*d*.

Bulletin signaletique d'entomologie médicale et vétérinaire, no. 5 (fourth quarter 1954). Paris: Office de la recherche scientifique et technique outre-mer. Price (Vol. II; 1955, six numbers) 1200 fr.

Proceedings of the New Zealand Ecological Society. No. 1: Report of the second annual meeting, 1953. No. 2: Report of the third annual meeting, 1954. Wellington, N.Z.

Megastigmus Flies Attacking Conifer Seed. By N. W. HUSSEY. London: H.M.S.O. (Forestry Commission Leaflet No. 8 revised 1954.). Price 6*d*.

Badgers in Woodlands. By E. G. NEAL. London: H.M.S.O. (Forestry Commission Leaflet No. 34). 1955. Price 9*d*.

ABSTRACTS

Abstracts are now appearing from the following journals and publications:

Agriculture
Ann. Appl. Biol.
Ann. Mag. Nat. Hist.
Antiquity
Biol. Rev.
Biometrika
Bird Study
Brit. Birds
Brit. J. Anim. Behav.
Bull. Ent. Res.
Bull. Mammal Soc. Brit. Is.
Coll. Repr. Scot. Mar. Biol. Ass.
Countryside
Discovery
Endeavour
Entomologist
Ent. Mon. Mag.
Ent. Rec.
Fish. Invest. Lond.
Ibis
J. Conchol.
J. Gen. Microbiol.
J. Hyg., Camb.
J. Mar. Biol. Ass. U.K.
J. Pomol.
J. Roy. Hort. Soc.
J. Sports Turf Inst.
Linn. Soc. Lond. Proc. & Trans.
Lond. Naturalist
Naturalist
Nature Lond.
New Biol.
Oryx
Parasitology
Proc. R. Irish Acad.
Proc. Malacol. Soc.
Proc. Prehist. Soc.
Proc. (Econ. & Sci.) Roy. Dublin Soc.
Proc. Zool. Soc. Lond.
Quart. J. Microsc. Sci.
Rep. Dove Mar. Lab.
Rep. East Malling Res. Stn
Rep. Mar. Biol. Stn. Pt Erin
R. Ent. Soc. Proc. & Trans.
Roy. Soc. Proc. & Trans.
Roy. Soc. Edinb. Proc. & Trans.
Salm. Trout Mag.
Sci. News
Scot. Agric.
Scot. Home Dept. Sci. Invest.
Scot. Nat.
Welsh J. Agric.

and the journals and proceedings of local natural history societies.

There remain a few journals, notably those covering forestry, which it is still impossible to abstract, and offers of assistance are still sought for these.

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, D. H. Chitty, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, Miss U. Grigg, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, Miss E. Nelmes, W. R. Pickering, J. L. Cloudesley Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter.**

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CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Barnes, H. (1952–3). The effect of light on the growth rate of two barnacles *Balanus balanoides* (L.) and *B. crenatus* Brug. under conditions of total submergence. *Oikos*, **4**, 104–111.

Growth rates, fertilization, and growth of embryos did not differ significantly between barnacles kept in daylight and those kept in the dark.

Clark, R. B. & Milne, A. (1955). The sublittoral fauna of two sandy bays on the Isle of Cumbrae, Firth of Clyde. *J. Mar. Biol. Ass. U.K.* **34**, 161–180.

A quantitative survey of the macrofauna between low water and 30 m depth, using a Robertson bucket dredge. Statistical treatment of the results reveals a degree of aggregation in some species.

Crisp, D. J. & Hobart, J. (1954). A note on the habitat of the marine Tardigrade *Echiniscoides sigismundi* (Schultze). *Ann. Mag. Nat. Hist.* (12) **7**, 554–560.

Feeding on algae on barnacles and similar surfaces throughout the intertidal zone, more commonly on more exposed shores. Map of localities. Tables of abundance in relation to shore, algal growth and season.

Evans, G. O. (1954). A revision of the genus *Thinoseius* Halbert, 1920. (Acarina–Laelaptidae). *Ann. Mag. Nat. Hist.* (12) **7**, 615–622.

Two species from under decaying intertidal seaweed.

Judges, E. C. & Southward, A. J. (1953). A note on the populations in the sea-water storage tanks at the Port Erin laboratory. *Rep. Mar. Biol. Sta. Pt Erin*, **65**, 24–27.

The storage tanks and their management are described: their nearest ecological equivalent is a deep pool near high water neaps. The fauna is largely derived from larvae or very small individuals entering with the water during pumping and rarely remains in the tanks for more than six months. Of the thirty-six species of animal found in the tanks during cleaning operations, twenty-seven were normally intertidal and most of the rest were subtidal: all but one of the subtidal species were known to have pelagic larvae. Notes on habits and growth rates of some species are added.

Lewis, J. R. (1954). The ecology of exposed rocky shores of Caithness. *Trans. Roy. Soc. Edinb.* **62**, 695–723.

The vertical and horizontal distributions of important plants and animals on exposed rocky shores in Caithness are described, and comparisons made with other shores of the British Isles. Factors which cause a marked uplift in the zonation of inter-tidal species in Caithness are considered.

Newell, G. E. (1954). The marine fauna of Whitstable. *Ann. Mag. Nat. Hist.* (12) **7**, 322–350.

Descriptions of habitats with brief accounts of their ecology. List of species from most phyla with short notes.

Oldroyd, H. (1954). The seaweed fly nuisance. *Discovery*, **15**, 198–202.

The life history of *Coelopa frigida* with discussion of the abnormal numbers in South coast and London areas in autumn 1953.

Pike, R. B. (1954). Notes on the growth and biology of the prawn *Spirontocaris lilljeborgii* (Danielssen). *J. Mar. Biol. Ass. U.K.* **33**, 739–747.

Includes notes on geographical distribution, occurrence in the Clyde, breeding, rates of growth and sexual characters of this species.

Smith, R. I. (1955). Salinity variation in interstitial water of sand at Kames Bay, Millport, with reference to the distribution of *Nereis diversicolor*. *J. Mar. Biol. Ass. U.K.* **34**, 33–46.

The occurrence of a zone of brackish interstitial water in the mid-tide sand of Kames Bay is recorded. Low salinity in the sand persists at high tide. The distribution of the polychaete *Nereis diversicolor* seems to be correlated with the presence of this low salinity belt.

Southward, A. J. (1953). Fluctuations in the sea and air temperatures at Port Erin during the past fifty years. *Rep. Mar. Biol. Sta. Pt Erin*, **65**, 28–31.

Sea and air temperatures taken during hours of daylight at Port Erin from 1903 to 1952 are examined in connexion with the rise in sea and air temperatures in the northern hemisphere over the last century. The scope of the measurements is discussed. The writer concludes that the sea temperature has risen by 0·2 to 0·4° C, and the air temperature by 0·5° C in fifty years. Most of the increase in air temperature was probably due to the influence of sunlight. Sea and air temperatures appeared to be closely related: the air temperature probably influenced the sea temperature rather than vice versa. The temperature rise in the Manx area appeared to be less than that recorded for south-west England.

Southward, A. J. (1954). Some notes on Manx medusae. *Rep. Mar. Biol. Sta. Pt Erin*, **66**, 17–22.

Brief observations are offered on twenty-five species of medusae from routine stramin and bolting silk hauls and from special hauls taken for the purpose. These observations confirm the impression gained by earlier workers that the medusa population of the Irish Sea is predominantly of northern character but contains a southern element in addition.

It seems likely that many medusae are liberated during the spring rise in temperature, but the occurrence of large shoals off the west coast of the Isle of Man in May and June is possibly due to water movements which tend to pen the animals against the shore rather than to the large numbers liberated.

Williams, G. (1954). Fauna of Strangford Lough and neighbouring coasts. *Proc. R. Irish Acad.* **56B**, 29–133.

Description of grounds. List of species with short notes. Most phyla included.

Yonge, C. M. (1953). Marine biological research and its practical importance. *Discovery*, **14**, 181–188.

Reviews marine biology in popular terms, as related to the needs of man, with particular reference to the problem of overfishing and the factors affecting changes in fish populations.

(*b*) Fresh Water

Coles, M. D. (1953). Camouflage in fishes. *Salm. Trout Mag.* **139**, 259–262.

Brief descriptions are given of protective mimicry in British freshwater and marine fish, together with a short account of the modern theory of the physiological causes thereof.

Hardy, E. (1953). The increasing grebe. *Salm. Trout Mag.* **139**, 237–244.

A discursive article in which relationship is sought between fluctuations in the population of various species of the genus *Podiceps* and various ecological factors. Of these factors it is suggested that the abundance or otherwise of freshwater fish transcends others such as the increase in area or number of suitable inland waters.

Harris, J. R. (1954). Trout fry territory. *Salm. Trout Mag.* **140**, 310–313.

Experiments with samples of trout fry artificially reared in acid and alkaline waters showed the establishment within each sample of a hierarchy dominated by one individual whose place, when removed, was taken by the next subordinate. When the dominant fish from each of two samples were placed together they attacked each other until exhausted. The explanation appears to lie in marked territorial behaviour.

Hawkes, H. A. (1955). The effects of insecticide treatment on the macrofauna populations, film accumulation and efficiency of sewage percolating filters. *Ann. Appl. Biol.* **43**, 122–133.

Includes a flotation method for the rough estimation of Collembola, and information on larval populations of *Anisopus fenestralis* related to food availability.

Lansbury, I. (1955). Some notes on the ecology of *Cymatia coleoptrata* Fabricius (Hem., Corixidae) in Hertfordshire and Kent. *Entomologist*, **88**, 66–67.

C. coleoptrata was the dominant corixid in four freshwater habitats differing widely in type, but all containing *Ceratophyllum* sp. This plant appears always to be present where the corixid occurs. The plants and other Heteroptera present in each of the four habitats are listed.

Leutscher, A. (1952). The habits of British amphibia. *Discovery*, **13**, 87–88.

Breeding behaviour of British species.

Mann, K. H. (1955). Some factors influencing the distribution of freshwater leeches in Britain. *Proc. Internat. Ass. Theor. App. Limnol.* **12**, 582–587.

Discusses influence of calcium content and area of standing waters on the distribution of British leeches. Some remarks on rate of movement of running waters.

Michael, P. (1953). Dragonflies and fish. *Salm. Trout Mag.* **139**, 254–258.

A short factual account of the role of the Odonata in food chains.

Rawlence, G. N. (1953). Fishing and freshwater biology in U.S.A. and Canada. *Salm. Trout Mag.* **139**, 263–267.

An account of various angling trips contains a report of experiments to ascertain the mechanism which enables Salmonidae to return to their native river. It appears that young fish are capable of remembering olfactory stimuli by volatile aromatic substances characteristic of their native river. This faculty is lost as the fish grow older. An account is also given of the favourable effect on artificially introduced stocks of rainbow trout (*Salmo irideus*) of raising the pH, by applications of slaked lime, of an acid lake.

Sankey-Barker, T. (1953). Notes on the feeding of trout in winter. *Salm. Trout Mag.* **139**, 234–236.

Despite a water temperature range of from 60° F down to 35° F trout were seen taking surface food on the Usk at Crickhowell on 83 days out of the total of 116 (no records for 9 days), between 10 November 1952 and 6 March 1953. Feeding, which appeared to be affected less by temperature than by high winds and discoloured or fast water, was confined largely to a few species of Plecoptera and Chironomids and the Ephemeroptera, *Baëtis rhodani* and *Rhithrogena haarupi*.

'Yeoman' (1954). Trout in still waters. *Salm. Trout Mag.* **140**, 314–321.

The effects on fauna and flora of impounding streams to form artificial water supplies are discussed. Initial changes following inundation give place in time to stable conditions similar to those in natural lakes, with the difference, however, that reservoirs are always subject to artificial changes of level at frequent intervals, with the result that fishing in reservoirs is usually less consistent than in lakes.

(*c*) Land

Alexander, W. B. (1952). The index of Heron population, 1951. *Brit. Birds*, **45**, 64–67.

The population of *Ardea cinerea* in the British Isles as a whole was standard for the first time since 1939. A table shows regional increases and decreases compared with standard years and with 1950.

Alexander, W. B. (1953). The index of Heron population, 1952. *Brit. Birds*, **46**, 100–103.

The results of the 1952 census are compared with those of 1951, and with the average in standard years. There was a slight increase in the country as a whole, as usual some areas showing increases, others decreases. The increases were most marked in areas which suffered most in 1947, and have been slowest in recovery. The overall index was 105 (standard = 100).

Alexander, W. B. (1954). The index of Heron population, 1953. *Brit. Birds*, **47**, 108–111.

The population in the country as a whole continued to be slightly above normal, but showed a slight decline compared with 1952, a trend that appears to be usual when the population has risen above standard.

Armstrong, E. A. (1952). The behaviour and breeding biology of the Shetland Wren. *Ibis*, **94**, 220–242.

It is shown that *Troglodytes t. zetlandicus* differs in several respects from *T. t. troglodytes*, and less markedly from other island races in behaviour. It is argued that the availability of food for the young is the reason why *zetlandicus* is monogamous, whereas *troglodytes* is not so in 50% of cases, and that such differences are of importance in speciation.

Armstrong, E. A. (1953). The behaviour and breeding biology of the Hebridean Wren. *Brit. Birds*, **46**, 37–50.

Habitat and nest-site preferences are compared with those of other races. Territories were found to be relatively large, twelve acres or more in extent. *Troglodytes t. hebridensis* appears usually to be monogamous.

Basden, E. B. (1954). Diapause in *Drosophila* (Diptera: Drosophilidae). *Proc. R. Ent. Soc. Lond.* (A), **29**, 114–118.

Published information on this subject and on reproductive arrest in *Drosophila* is reviewed. Larvae of *D. deflexa* remain in diapause during the winter and pupate in the spring. Time of pupation coincides with a period when minimum temperature is 10° C or above. At 18° C some larvae do not enter diapause and the proportion has been increased by selection. Females of *D. subobscura* (and probably of *D. obscura* and *D. tristis*) pass the winter in a state of reproductive arrest but are capable of immediate reproduction when kept with males at 18° C.

Campbell, B. (1955). The breeding distribution and habitats of the pied fly-catcher (*Muscicapa hypoleuca*) in Britain. Part 2. The breeding habitats. *Bird Study*, **2**, 24–32.

Lists known breeding under Watsonian provinces. The most favoured habitats are highland valleys and foothills up to the tree limit, there being usually no continuous shrub layer and field layer. Proximity to water is not essential. Except in mature woodland nest boxes are essential.

Cloudsley-Thompson, J. L. (1952). The biology of centipedes and millipedes. *Discovery*, **13**, 18–21.

An account of recent work on economics, behaviour and life history.

Cloudsley-Thompson, J. L. (1953). The biology of hunting spiders. *Discovery*, **14**, 286–289.

Feeding habits and prey of the British Salticidae.

Colley, R. J. (1954). Biological control. *Discovery*, **15**, 315–320.

A general review: discusses some British species.

Collingwood, C. A. (1954). The biology of *Epipolaeus calignosus* (Col., Curculionidae). *Ent. Mon. Mag.* **90**, 169–172.

Observations on the seasonal history of this pest of hops in Worcestershire and Herefordshire, with descriptions of all stages.

Collyer, E. & Kirby, A. H. M. (1955). Some factors affecting the balance of phytophagous and predacious mites on apple in south-east England. *J. Hort. Sci.* **30**, 97–108.

Typhlodromid mites can only play a decisive role in the control of *Metatetranychus ulmi* when the ratio of the pest to predators is low. Typhlodromid population density should exceed that of *M. ulmi* until mid-May, and this is not usually possible when winter or spring washes have been used.

Cott, H. B. (1953–4). The exploitation of wild birds for their eggs. *Ibis*, **95**, 409–449, 643–675; **96**, 129–149.

Besides estimating the annual egg crop obtained from a great number of species, the effects of egging on various species are reviewed, and the necessity for the rational control of the practice is stressed.

Coulson, J. C. & White, E. (1955). Abrasion and loss of rings among sea-birds. *Bird Study*, **2**, 41–44.

Abrasion of rings on kittiwakes occurs at the rate of 8·6% loss of weight per year, the rings becoming illegible after about four years. Correlative confirmation is offered for ringed manx shearwaters. Investigation of the effects of corrosion and abrasion is called for since the rings become illegible before the life-span of the wearer is completed.

Cranbrook, Earl of (1955). Water rat remains in a Bronze Age site. *Bull. Mammal Soc. Brit. Is.* **3**, 2–4.

Skull fragments from (i) a Bronze Age site at Wilson Scar, Westmorland, where they were associated with cheek teeth believed to be of red deer, and (ii) a Roman fort at Newstead, near Melrose, said to have been 'found amongst produce of the chase' suggest that a water rat smaller than *Arvicola terrestris amphibius* may have existed in south Scotland and north England until comparatively recently, and that it may have been an article of human food, as was *Glis glis* to the Romans.

Crisp, G. & Lloyd, Ll. (1954). The community of insects in a patch of woodland mud. *Trans. R. Ent. Soc. Lond.* **105**, 269–314.

This survey shows that larvae of Chironomidae, Tipulidae, Psychodidae and Ceratopogonidae are dominant both in variety and in numbers. A list of insects is given, together with the collection data and its analysis. Biological notes are provided and a comparison is drawn between this habitat and the macrofauna of sewage filters.

Crook, J. H. (1953). An observational study of the gulls of Southampton Water. *Brit Birds*, **46**, 385–397.

An outline study of the roosting behaviour and dispersal of gulls in the estuary. The different feedin habitats of *Larus ridibundus* are described.

Cuthbertson, E. I., Foggitt, G. T. & Bell, M. A. (1952). A census of Common Sandpiper in the Sedbergh area, 1951. *Brit. Birds*, **45**, 171–175.

About 60 out of 300 miles of river and beck along the River Lune and its tributaries held *Actiti hypoleucos*. The density was greatest in the low river valleys, and limestone areas and streams with a fa greater than 200 feet per mile were avoided. The sixty miles occupied carried 101 pairs.

Duffey, E., Locket, G. H. & Millidge, A. F. (1954). On some spiders collected in Eas Suffolk and Essex. *Ann. Mag. Nat. Hist.* (12) **7**, 474–478.

Short notes on the habitats of several species. Three species new to Britain.

Ellenby, C. (1954). The eelworm and the potato. *Discovery*, **15**, 34–36.

Six resistant varieties of potato were found out of some 1200.

Emmet, H. J. (1954). A swallow colony. *Countryside* (N.S.), **17**, 27.

The number of nesting pairs at the Vicarage, Stoughton, near Chichester declined from 1934 to 195 after which no further breeding took place.

Fisher, J. (1952). A history of the Fulmar *Fulmarus* and its population problems. *Ibis*, 94 334–354.

The distribution of *Fulmarus glacialoides* (Antarctic), *F. glacialis rodgersii* (Pacific), and *F. g. glacial* (Atlantic) is discussed. The increase and spread of the Atlantic Fulmar dates from the mid-eighteent century, and in Britain from 1878; and is described in detail. It is suggested that this was made possibl by man through the provision of food, first whale carcasses, later trawler waste and offal, so that th species is now partly a dependant of man. The writer rejects the suggestion that adults do not bree every year, but thinks it probable that it may sit on a nest site for four or five years before it is adult a the age of seven, eight, or nine years.

Free, J. B. (1955). Queen production in colonies of bumblebees. *Proc. R. Ent. Soc. Lond* (A) **30**, 19–25.

Queen bumblebees have been induced to found colonies by confining them with varying numbers o workers and an abundance of food. When a sufficient number of workers were present to help the quee some of the first eggs laid by her developed into queens. Such experimental work supports the vie that the production of queens in bumblebee colonies is brought about by the reduction in the larv worker ratio with the result that an increased amount of food becomes available per larva. Includ a discussion of the factors which lead to the production of queens in naturally occurring colonies.

Gee, E. P. (1951). The Chillingham Cattle. *Oryx*, **1**, 102–103.

A summary of the formation of the Chillingham Wild Cattle Association, Ltd., and of the history o the herd since the severe winter of 1946–47.

George, W. (1953). Some animal reactions to variations of temperature. *Endeavour*, 12 101–105.

Physiological adaptations, Bergmann's, Allen's and Gloger's rules and the effects of temperature o the expression of genes and rate of mutation are discussed. Higher temperatures favour more rap evolution than lower ones.

Gillham, M. E. (1953). An annotated list of the flowering plants and ferns of Skokholm Island, Pembrokeshire. *Northw. Nat.* (N.S.) **1**, 539–557.

An annotated list. The distribution of many species depends on rabbits and other biotic factors.

Goodbody, I. M. (1952). The post-fledging dispersal of juvenile titmice. *Brit. Birds*, **45**, 279–285.

All the young of *Parus caeruleus* and *P. major* in an area of mixed deciduous woodland near Oxford were colour ringed in 1950, and regular counts of ringed and unringed young birds were made in the study area and an adjacent strip of woodland until mid-September. An explosive dispersal within a week or two of fledging is suggested.

Hewson, R. (1953). The Red Squirrel—*Sciurus vulgaris leucourus* Kerr in Easter Ross. *Northw. Nat.* (N.S.) **1**, 493–496.

There was a great expansion of numbers from 1850 to 1900, and there has been an equally striking decline since then, especially since 1933. Neither destruction by man nor felling of woodlands seems to have been responsible; there is considerable similarity between the curves for squirrels killed and for mountain hares (*Lepus timidus*) killed during the period 1900–40.

Hewson, R. (1954). The mountain hare in Scotland in 1951. *Scot. Nat.* **66**, 70–88.

The results of a survey, mainly by questionnaire to gamekeepers. In 1951 *Lepus timidus* was increasing in most parts of Scotland, and commonest in the eastern Highlands. On eight estates where figures for both species were available the major peaks in hares roughly coincided with those for red grouse.

Johnson, C. G. (1953). The aerial dispersal of aphids. *Discovery*, **14**, 18–22.

Outlines methods used for the collection of aerial insects at regular periods and at pre-determined altitudes, and indicates daily variations in the density of aphid populations.

Kirk, F. L. (1954). Outline study of the natural history of Roughton Moor. *Trans. Lincs. Nat. Union*, **13**, 175–179.

Includes brief notes on vertebrates, beetles and Lepidoptera, of a lowland heath near Woodhall Spa.

Knight-Jones, E. W. (1955). The gregarious setting reaction of barnacles as a measure of systematic affinity. *Nature, Lond.* **175**, 266.

The setting of *Balanus balanoides* is found to be selective. Same species most favoured, same family somewhat favoured, whilst members of other families have no apparent stimulatory effect.

Lack, D. (1954). The stability of the Heron population. *Brit. Birds*, **47**, 111–121.

The annual censuses in three regions of England which have been nearly complete in a number of years since 1928 show that the population of *Ardea cinerea* decreases markedly after a severe winter, and recovers rapidly to nearly its former level. The general level of numbers has changed gradually, having risen in some areas and fallen in others. The size and spacing of heronries varies with the locality and habitat, and may change with time.

Lack, D. (1955). The summer movements of swifts in England. *Bird Study*, **2**, 32–40.

Of eighteen records since the war of summer movements of swifts involving between 1000 and 6000 birds, nearly all have occurred in the east. Seventeen proceeded between south and west, sixteen of these being against the wind and one south with a west wind. In over two-thirds of the cases the movement was away from a major depression, the birds usually being to the south, sometimes to south-east of it. Only two movements occurred under high pressure and settled weather. The view that it is an innate response to weather conditions is favoured by the author.

Leutscher, A. (1953). The timid viper. *Countryside* (N.S.), **16**, 337–342.

Liversidge, D. (1952). Australia's war against the rabbit. *Discovery*, **13**, 190–195.

Myxomatosis and rabbit control: transmission of the virus by *Aedes*, *Culex*, etc.

Marshall, A. J. (1952). Non-breeding among Arctic birds. *Ibis*, **94**, 310–333.

A study made on Jan Mayen Island in 1947. Field observations suggested that sexually mature birds do not breed owing to lack of safe nest-sites, and to food shortage, the causes differing in different species. Laboratory examination of the gonads of breeding and non-breeding birds suggests that the gonad cycle of non-breeders of both sexes does not develop fully, the probable reason being that the environment does not present the appropriate stimuli.

Matheson, C. (1953). The Partridge in Wales: a survey of gamebook records. *Brit. Birds*, **46**, 57–64.

The records of thirteen estates were taken, some being unbroken for 50–70 years, and one from 1854 to 1951: most are from the 1870's, but a few go back to the 1820's before intensive preserving introduced artificial factors. The average interval between population peaks is 9·5 years, compared with 8·2 in England. Possible causes of the decline in the population during the past thirty years are suggested.

Matthews, L. H. (1954). The hibernation of animals. *Discovery*, **15**, 437–442.

A review of the phenomenon in dormice and hedgehogs with reference to cyclic changes in glandular activity.

Michaelis, H. N. (1954). The effect of winter floods on certain species of Lepidoptera. *Ent. Rec.* **66**, 257.

Numbers of *Crambus pratellus* emerging in 1954 from a field that was flooded for three weeks during January–February were greatly reduced, possibly by 50%, whereas those of three other common species (*C. culmellus*, *Cnephasia incertana* and *Elachista cerusella*) were unaffected. Of twenty larvae of the last species, only 10% were parasitized, whereas normal parasitism on this ground was 25–35%.

Miles, M. (1954). Field studies on the influence of weather on egg-laying by the cabbage root fly, *Erioischia brassicae* Bché. II. *Ann. Appl. Biol.* **41**, 586–590.

Oviposition by *E. brassicae* was most active between 65–70° F, and declined during prolonged periods of higher temperatures. The annual cycle consists of two generations and a partial third; overwintering puparia come from second and third generation larvae.

Morley, A. (1953). Field observations on the biology of the Marsh Tit. *Brit. Birds*, **46**, 233–238, 273–287, 332–346.

The present paper is the fifth of a series describing observations on a population of *Parus palustris* in a 50-acre tract of a Berkshire wood, and includes sections on social life, aggression and territorial behaviour, some aspects of breeding behaviour, and roosting behaviour.

Morley, D. W. (1953). The organisation of the ant colony. *Discovery*, **14**, 45–49.

Myres, M. T. (1955). The breeding of blackbird, song thrush and mistle thrush in Great Britain. Part I. Breeding seasons. *Bird Study*, **2**, 2–24.

Analysis of nest record cards for 9500 nests of the three species between 1948 and 1953, with a discussion of the limitations of the nest record scheme. The pattern of breeding varies from year to year, the first clutches in March being controlled by temperature, but not those later in the year. The three to four peaks of egg-laying shown by all three birds coincide.

Pearce, E. J. (1954). Notes on the life-history and habitat of *Cardiophorus asellus* Erichson (Col., Elateridae). *Ent. Mon. Mag.* **90**, 204–205.

Information on seasonal occurrence, with data on abundance in two types of habitat obtained by a modification of a sieving method (see 1945, *Ann. Appl. Biol.* **32**, 148–163), which is described.

Savidge, J. P. (1954). The effect of weather conditions upon animals and plants, 1953. *Proc. Liverpool Nat. Fld. Cl.* **1953**, 9–11.

Brief phenological notes on birds, butterflies and moths, for the Liverpool district.

Shaw, M. W. (1955). Preliminary studies on potato aphids in north and north-east Scotland. *Ann. Appl. Biol.* **43**, 37–50.

Population studies. Populations of *Myzus persicae* develop sooner and reach greater numbers near urban areas; *M. persicae* was the predominant aphid at most sites, although *Aulacorthum solani* was more numerous north of Inverness. Oviparae of *A. solani* were found on *Ranunculus repens* and *Rubus idaeus*. *Macrosiphum euphorbiae* was present in small numbers in many areas, and *Aphis nasturtii* was scarce, as were its winter hosts.

Southwick, C. H. & Southern, H. N. (1955). A note on the abundance of harvest mice (*Micromys minutus*) in Hampshire and Berkshire. *Bull. Mammal Soc. Brit. Is.* **3**, 9–10.

Records fifty-one harvest mice during the winter 1954–55 from eight of twelve ricks examined, giving sexes, measurements and weights. Local opinion remarked on the abundance of the mice, and this is confirmed by the estimated figures for Berkshire ricks of twenty-one (actual number fourteen), compared with only four recorded by Southern, Chitty, Middleton, Venables and others from several hundred ricks in Oxfordshire and Berkshire during the 1940's.

Stewart, J. (1954). Hypomagnesemia and tetany of cattle and sheep. *Scot. Agric.* **34**, 68–73.

Symptoms of magnesium deficiency, differentiated from true tetany, appear to be related to feeding, but exact correlation with seasonal grass conditions has yet to be demonstrated.

Summers-Smith, D. (1952). Breeding biology of the Spotted Fly-catcher. *Brit. Birds*, **45**, 153–167.

An analysis of data on more than five hundred nests, the principal source being Nest Record cards of the British Trust for Ornithology. The conclusion is drawn that *Muscicapa striata* can rear a brood of five successfully in Britain only when conditions are very favourable. No significant difference in nesting success with season was detected.

Taylor, C. E. (1955). Growth of the potato plant and aphid colonization. *Ann. Appl. Biol.* **43**, 151–156.

Successful colonization is greatly dependent upon the physiological development of the plant. Infestations by aphids may be interpreted between potato varieties and within a variety by reference to vegetative growth.

Tegner, H. (1955). Roe Fawns. *Oryx*, **3**, 30–32.

An account of the frequency of twins and triplets among fawns of the Roe Deer in Northumberland, Scotland and Sweden.

Urbain, A. & Nouvel, J. C. G. (1954). On keeping wild animals in zoos. *Endeavour*, **13**, 184–189.

Habitat, diet, pathology and psychology of captive birds and mammals are discussed and the fallacy of the belief that animals in the wild are free to roam at will is exposed.

Venables, L. S. V. & Venables, U. M. (1952). The Blackbird in Shetland. *Ibis*, **94**, 636–653.

Turdus merula has bred on Shetland for about 70 years. The breeding density was estimated over nine square miles at about one pair to 300 acres, from which a total Shetland breeding population of 1230 pairs can be assumed. Eggs are laid later, and clutches are significantly larger than in England. Ringing has shown that the population does not move outside Shetland. Birds from Norway and Denmark occur as passage migrants, and some remain all the winter.

Wallace, H. R. (1954). Notes on the biology of *Arhopalus ferus* Mulsant (Coleoptera: Cerambycidae). *Proc. R. Ent. Soc. Lond.* (A) **29**, 99–113.

Life history of *Arhopalus* is described, and the relationships between larval growth and diapause, and temperature and the time of pupation are discussed. Length of larval life varies from two years in slightly decayed wood to five years in highly decayed wood; the weight increment of the larvae decreases as the wood decays.

Wannop, A. R. (1955). The Hill Farming Research Organisation. *Scot. Agric.* **34**, 177–180.

Directs attention to the need for vegetative studies in work to improve the winter performance of hill sheep.

Yapp, W. B. (1953). The bird community of the fell woods of the English Lake District. *Northw. Nat.* (N.S.) **1**, 503–512.

Seven woods, at altitudes exceeding 1000 ft (305 m) have a characteristic community of birds, most of which nest regularly or occasionally on the ground. All have a diet very largely restricted to insects, a habit for which the term eteoentomophagous is proposed. There is almost complete migration from the woods in autumn.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Barnes, H. (1953). Underwater television and research in marine biology, bottom topography and geology. Part 1. A description of the equipment and its use on board ship. *Dtsch. hydrogr. Z.* **6**, 123–133.

Betts, M. M. (1954). Experiments with an artificial nestling. *Brit. Birds*, **47**, 229–231.

Describes the construction of an artificial nestling which was used successfully in collecting samples of the food brought to a nest of *Muscicapa hypoleuca* in a specially constructed nest-box.

Brownlow, H. G. (1952). The design, construction and operation of Heligoland traps. *Brit. Birds*, **45**, 387–399.

Heligoland traps for catching birds for ringing are described in greater detail than in previously published literature, and the paper is fully illustrated with diagrams.

Busvine, J. R. (1955). Simple methods for rearing the cricket (*Gryllulus domesticus* L.) with some observations on speed of development at different temperatures. *Proc. R. Ent. Soc. Lond.* (A) **30**, 15–18.

Godfrey, G. K. (1954). Use of radioactive isotopes in small-mammal ecology. *Nature, Lond.* **174**, 951–952.

A description of the method employed in a study of the movements of the field vole (*Microtus agrestis*) and the mole (*Talpa europaea*).

Hammad, S. M. (1955). The immature stages of *Pentarthrum huttoni* Woll. (Coleoptera: Curculionidae). *Proc. R. Ent. Soc. Lond.* (A), **30**, 33–39.

An account of the life history is followed by a description of the immature stages.

Haskey, H. W. (1954). A general expression for the mean in a simple stochastic epidemic. *Biometrika*, **41**, 272–275.

An extension of Bailey's 1950 paper (*Biometrika* **37**, 193–202) allowing calculations for rather larger numbers. The course of an epidemic in a population of thirty individuals is given numerically.

Hickin, N. E. (1954). Larvae of the British Trichoptera.–43. *Proc. R. Ent. Soc. Lond.* (A) **29**, 89–92.

Larva of *Grammotaulius atomarius* is described and figured, and a figure given of the adult.

Hickin, N. E. (1954). Larvae of the British Trichoptera.–44. *Proc. R. Ent. Soc. Lond.* (A) **29**, 93–95.

Larva of *Lype phaeopa* is described and figured, and a figure given of the adult.

Hickin, N. E. (1954). Larvae of the British Trichoptera.—45. *Proc. R. Ent. Soc. Lond.* (A) **29**, 96–98.

Larva of *Limnephilus centralis* is described and figured, and a figure of the adult is given.

Irwin, J. O. (1954). A distribution arising in the study of infectious diseases. *Biometrika*, **41**, 266–268.

An unusual form of the hypergeometric distribution gives a good fit to the number of cases of measles in households in one epidemic. It is derived by assuming that the probabilities of infection of the susceptibles in a household are correlated, and that the correlations are all equal. (This is the 'general solution' mentioned by Greenwood (1949) *Biometrika*, **36**, 1–8.)

Johnson, C. G. (1953). Aerial dispersal of aphids. *Discovery*, **14**, 18–22.

A review of recent work using aerial tow-nets and suction traps.

Johnson, C. G. & Taylor, L. R. (1955). The development of large suction traps for airborne insects. *Ann. Appl. Biol.* **43**, 51–62.

Large traps, incorporating fan units, have been introduced for use in exposed situations where insect densities are very low or where winds are strong. Because of the large sample obtained, they also enable transient density fluctuations to be followed.

Merrington, Maxine (Arranger) **(1955).** Biometrika Index. Author Index: Vols. 1–40 (1901–1953). Subject Index: Vols. 1–37 (1901–1950). (University College, London: 6*s*.)

Moore, N. C. (1953). A balance for weighing tits without capture. *Brit. Birds*. **46**, 103–105.

A device for fixing outside a window operated by an observer in the room. It can be adjusted for loss of weight of the bait. The description is illustrated with a diagram, and with a photograph showing the balance in operation.

Roe, K. M. (1955). Genus *Paraphyllopodopsyllus* Lang. (Copepoda Harp.). Two new species—*P. hibernicus* and *P. hardingi*. *Proc. R. Irish Acad.* **57**(B), 131–139.

Well illustrated description of two new species of littoral harpacticid copepods from Co. Dublin, recording the genus for the first time from the northern hemisphere.

Sands, W. A. (1954). *Deraeocoris olivaceus* (F.) (Hem., Miridae) new to Britain. *Ent. Mon. Mag.* **90**, 301.

Includes a description of the adult and a key separating it from other British species.

Simms, E. & Wade, G. F. (1953). Recent advances in the recording of bird-songs. *Brit. Birds*, **46**, 200–210.

The advantages of the magnetic tape over the disk record are described, and of the parabolic reflector over the dynamic coil for use with it. Masking of low intensity sounds by surface noise is avoided by the tape recorder, so that low conversational calls, and even the footfall of the badger have been successfully recorded. Its greater range renders disturbance of the birds unnecessary, and the notes of birds in flight up to 200 yards away have been successfully recorded with a 36-inch reflector.

Spencer, K. A. (1954). Notes on the British Agromyzidae (Dipt.). III. *Ent. Mon. Mag.* **90**, 217–218.

Liriomyza eupatoriana n.sp. is described from specimens found mining in the leaves of *Eupatorium cannabinum* in Wiltshire. A description of the mine and a modification of Hendel's key to accommodate this species are also given.

Thompson, H. R. (1954). A note on contagious distributions. *Biometrika*, **41**, 268–271.

A method, due to J. H. Darwin, of producing a large number of different contagious distributions. Neyman type A and type C and an approximation to the negative binomial are special cases. Gives arguments against using Thomas' 'double Poisson' distribution.

Turrill, W. B., Hewer, H. R., Anderson, M. S. & Willatts, E. C. (1954). *The cartographical presentation of biological distributions*. 35 pp. London: R. Geographical Society.

Discusses various methods of presenting distributional data in map form.

Whittle, P. (1954). On stationary processes in the plane. *Biometrika*, **41**, 434–449.

Fitting two-dimensional autoregressive models to field data. Exemplified by data on the yields of wheat and of orange trees.

Williamson, K. (1954). The Fair Isle apparatus for collecting bird ecto-parasites. *Brit. Birds*, **47**, 234–235.

By means of a cylinder with bottles for chloroform attached to it ecto-parasites are removed from all birds trapped for ringing so that both qualitative and quantitative studies can be made.

Yarrow, I. H. H. (1955). Some ways of distinguishing between the two common wasps *Vespula germanica* (Fabricius) and *Vespula vulgaris* (Linnaeus). *Entomologist*, **88**, 5–9.

Some morphological and basic colour characters for the separation of specimens showing variations from the usual colour patterns.

3. PARASITES

Allan, R. M. & Shanks, P. L. (1955). Rabbit fleas on wild rabbits and the transmission of myxomatosis. *Nature, Lond.* **175**, 692.

Census of *Spilopsyllus cuniculi* on wild rabbits in the region of Aberdeen, through 1954. Laboratory experiments have shown *S. cuniculi* and *Ixodes reduvius* can be vectors.

Arthur, D. R. (1953). Economic importance of ticks. *Discovery*, **13**, 379–383.

Importance of *Ixodes ricinus*.

Basden, E. B. & Goodey, J. B. (1955). A nematode parasite of *Drosophila*. *Nature, Lond.* **175**, 431–432.

Aphelenchulus sp. from the abdomens of flies. All stages found. Eelworm larvae often abundant in the ovaries which were then stunted, but not observed in testes.

Bolster, G. C. (1954). The biology and dispersal of *Mytilicola intestinalis* Steuer, a copepod parasite of mussels. *Fish. Invest., Lond.* (2) **18**, (6), 1–30.

Records *Mytilicola* from several scattered stations on the west coast of Britain, mainly near shipping ports. The planktonic stage being brief, natural spread is slow and the chief agency has been infested mussels on ships' bottoms. The animal breeds in waters above 6° C, reproduction being interrupted during February and March on the east coast but continuous in the Channel and on the west coast. The relations between infection and tidal limits, temperature, salinity, turbulence and current are discussed, as is also the possibility of heavy infestation of oysters.

Bull, P. C. (1955). Population regulation in rabbit nematodes. *Nature, Lond.* **175**, 218–219.

Trichostrongylus retortaeformis shows infestation size decreasing after second weight group (400–599 g). But wide infection size range in each group . . . and differences according to locality. Discussions of these findings in relation to those of allied works, of Elton on *Apodemus* and Evans, W., on *Graphidium strigosum* from *Oryctolagus*.

Cole, H. A. & Hancock, D. A. (1955). *Odostomia* as a pest of oysters and mussels. *J. Mar. Biol. Ass. U.K.* **34**, 25–31.

A description of the serious damage to oysters caused by *Odostomia eulimoides*, a pyramidellid gastropod. An incidence of 30% infection was found in 3-year-old oysters in the River Colne, Essex. *Chrysallida obtusa*, another pyramidellid, is recorded for the first time as a parasite of oysters. The effects of *Odostomia scalaris* on mussels are similar to those of *O. eulimoides* on oysters.

Ellenby, C. (1955). The seasonal response of the potato-root eelworm *Heterodera rostochiensis* Wollenweber: emergence of larvae throughout the year from cysts exposed to different temperature cycles. *Ann. Appl. Biol.* **43**, 1–11.

Larval emergence from air-dried cysts kept at different temperatures varied considerably, but there was no evidence of a dormancy period.

Fraser, F. C. (1954). High mortality of *Euphydryas aurinia* (Rott.) (Lep., Nymphalidae) from parasitisation by *Apanteles bignelli* Marsh. (Hym., Braconidae). *Ent. Mon. Mag.* **90**, 253.

Larvae of this nymphalid were extremely numerous in Dorset in 1954, but about 80% were parasitized by *A. bignelli*. This factor is believed to be the main cause of the periodical scarcity of the butterfly.

Gotto, R. V. (1955). The occurrence of *Lernaeopodina cluthae* (T. Scott) on a new host, *Raia maculata* Montagu. *Irish Nat. J.* **11**, 255–256.

Hobart, J. & Whalley, P. E. S. (1954). Occurrence of a species of *Ornithodoros* in Britain. *Nature, Lond.* **174**, 936.

Reports an *Ornithodoros* species of the *talaje* group from Puffin Island in the Menai Straits (N. Wales).

Hussey, N. W. (1955). The life-histories of *Megastigmus spermotrophus* Wachtl (Hymenoptera: Chalcidoidea) and its principal parasite, with descriptions of the developmental stages. *Trans. R. Ent. Soc. Lond.* **106**, 133–151.

Contains details of copulation, oviposition behaviour, larval instars and the phenology of the Chalcid and the host tree—the Douglas Fir. Results of experiments on the extended diapause of the larvae are recorded. A key is provided to three parasites—*Trichomalus* sp., *Anogmus strobilorum* Thompson and *Amblymerus* ? *apicalis* Thomson. The latter appears to be the principal parasite and the life-history, habits and the larval stages are described.

Jeffree, E. P. (1954). Acarine disease of the honeybee and temperature. *Nature, Lond.* **175**, 91.

Significant direct correlations between acarine incidence and temperature.

Jones, F. G. W. (1954). First steps in breeding for resistance to potato-root eelworm. *Ann. Appl. Biol.* **41**, 348–353.

Eggs and larvae of *Heterodera rostochiensis* are reduced from about 1500 per g of soil to about 100 per g when eelworm-resistant potato strains are grown instead of susceptible varieties.

Owen, D. F. (1954). *Protocalliphora* in birds' nests. *Brit. Birds*, **47**, 236–243.

The larvae of *Protocalliphora* are parasitic on nestling birds. Instances of fatal infestations are given, and it is suggested that these are exceptional. American, European and other records are summarized, and a list of the known hosts of *P. azurea* in Britain is given.

Poulding, R. H. (1952). Five cases of aspergillosis in immature gulls. *Ibis*, **94**, 364–366.

Dissections of gulls found dead at a large roost from October 1948 to August 1951 revealed the presence of *Aspergillus fumigatus* in three first-winter and one second-winter *Larus argentatus* and one first-winter *Larus fuscus*. Macro- and microscopical symptoms are described, and the mould was grown from four cases. The source of the infection was not traced, but it is suggested that it may be grain.

Stamp, J. T., Dunn, A. M. & Watt, J. A. A. (1955). Lamb losses from worms: *Nematodirus* infestation. *Scot. Agric.* **34**, 213–215.

The intestinal worms *Nematodirus battus* and *N. filicollis* have caused losses of Border lambs for a number of years. In 1954 severe outbreaks were more widespread in Scotland and in parts of England, and gave rise to the misconception that a new disease had been encountered.

Thompson, G. B. (1954). Contributions towards a study of the ectoparasites of British birds and mammals.—No. 3. *Ann. Mag. Nat. Hist.* (12) **7**, 438–447.

Lipoptena cervi (Diptera, Hippoboscidae) from red and roe deer. Identification, bibliography and history, life history, British distribution.

Thompson, G. B. (1955). Contributions towards a study of the ectoparasites of British birds and mammals.—No. 4. *Ann. Mag. Nat. Hist.* (12) **8**, 25–35.

Hippobosca equina (Diptera). Bibliography, life history, distribution.

Thompson, G. B. & Arthur, D. R. (1955). Records of ticks collected from birds in the British Isles.—2. *Ann. Mag. Nat. Hist.* (12) **8**, 57–60.

Supplement and corrections to a paper by the same authors in the same journal (1953, (12) **6**, 797–800).

Winslow, R. D. (1954). Provisional lists of host plants of some root eelworms (*Heterodera* spp.). *Ann. Appl. Biol.* **41**, 591–605.

Tabulated host ranges of *H. schachtii*, *H. schachtii* var. *trifolii*, *H. cruciferae*, *H. rostochiensis*, *H. carotae*, *H. humuli*, *H. major*, and *H. göttingiana*.

Woodroffe, G. E. (1954). An association between *Berytinus crassipes* (Herr.-Sch.) (Hem., Neididae) and chickweed (*Cerastium* spp.). *Ent. Mon. Mag.* **90**, 213.

This species, which was not hitherto associated with any particular food plant, was found on three occasions on stunted or rabbit-grazed plants of *Cerastium*, on two of them on ant-hillocks.

4. FOOD AND FOOD HABITS

Allen, A. A. (1954). *Cantharis nigricans* Müll. (Col.) preying on *Dasytes aerosus* Kies. (Col.); and a note on a habit of *C. rustica* Fln. *Ent. Mon. Mag.* **90**, 189.

Allen, A. A. (1954). *Phyllobius* (*Nemoicus*) *oblongus* L. (Col., Curculionidae) on *Acer* and *Tilia* spp. *Ent. Mon. Mag.* **90**, 221.

The primary food plant of this pest of fruit trees appears to be elm, both *Ulmus procera* and *U. glabra* being attacked. In Herefordshire, however, it was found established on *Tilia cordata*, *T. vulgaris* and *Acer campestre* as well as on *U. glabra*.

Allen, A. A. (1954). *Hypophloeus bicolor* Ol. (Col., Tenebrionidae) abnormally (?) associated with the fungus *Daldinia*. *Ent. Mon. Mag.* **90**, 234.

This beetle, here recorded for the first time from Shropshire, occurred in and about *D. concentrica* on an old, fallen ash trunk. It probably originally preyed on *Hylesinus crenatus*, the galleries of which riddled the bark, and when this scolytid disappeared preyed on other larvae, such as *Biphyllus lunatus* and *Litargus connexus*, which were abundant.

Barnes, H. F. (1954). Gall midges living in white clover flowers. *Entomologist*, **87**, 258–264.

A survey of the cecidomyiids in flower heads of red and white clover established that a species of *Dasyneura* is widely distributed in white clover in England and Wales. The adults emerged during July–October and mated successfully with others reared from red clover. Females from white clover oviposited in open florets of white and red clover but not in unopened florets of red. Lists of the cecidomyiid genera reared from red and white clover flowers and a description of the rearing method employed are given.

Colyer, C. N. (1954). Further emergences of *Conicera tibialis* Schmitz, the 'Coffin Fly' (Diptera, Phoridae). *Entomologist*, **87**, 234.

A second generation of adults appeared in August over the soil in which a dead dog was buried [see 1954, *Entomologist*, **87**, 129–32 and abstract in 1955, *J. Anim. Ecol.* **24**, 214]. Numerous earthworm-tunnels extending between the surface of the soil and the corpse provided a direct means of access to the latter for adult Phorids.

Gradwell, G. R. (1954). Feeding habits of two Carabid beetles. *Ent. Mon. Mag.* **90**, 231.

Carabus problematicus gallicus is recorded feeding on a small earthworm and *Feronia madida* v. *concinna* attacking a female *Forficula auricularia*.

Green, J. (1954). The food, predators and a parasite of *Bembidion laterale* (Samouelle) (Col., Carabidae). *Ent. Mon. Mag.* **90**, 226–227.

Observations were made at an estuary in Carmarthenshire where this carabid was so numerous in April, 1954, that 146 entered a patch of sand 20 cm square in 15 min. The beetle fed on the larvae of a dolichopodid and the amphipod, *Corophium volutator*, and was preyed on by ringed plover (*Charadrius hiaticula*) and dunlin (*Calidris alpina*). Thirty-nine of the 146 captured were infected by a fungus identified as *Laboulbenia pedicillata*.

Green, J. (1954). A note on the food of *Chaetogaster diaphanus*. *Ann. Mag. Nat. Hist.* (12) **7**, 842–844.

A carnivorous freshwater oligochaete. Apparently feeds on suitable sized invertebrates in proportion to their frequency, except that hydracarines are rejected.

Harrison, J. W. Heslop (1954). *Carsia paludata* Thunberg, its distribution and food plants. *Entomologist*, **87**, 247–248.

In Upper Teesdale and several islands of the Hebrides, this moth is associated with *Vaccinium myrtillus*, and *V. oxycoccus* and *V. vitis-idaea*, which are usually regarded as its food plants, are absent or present only in small quantities.

Jones, R. (1954). The food of the whiting, and a comparison with that of the haddock. *Scot. Home Dept. Mar. Res.* **2**, 1–34.

Analysis of stomach contents of 4300 whiting and 900 haddock between November 1948 and December 1949 and sorted into 5 cm groups. Whiting are active predators feeding mainly on fish and crustacea, with annelids and molluscs as very secondary items and echinoderms very rarely so. *Ammodytes* is the most important food fish of smaller whiting, *Gadus esmarkii* of the larger fish. The principal crustacean is *Crangon allmanni*, but young whiting are more catholic than older fish in the choice of crustacea. The latter also eat a larger proportion of fish. Haddock are exclusively bottom feeding, eating fish only sporadically, and taking principally echinoderms, annelids, molluscs and crustacea. Methods of statistical analysis are discussed.

Parmenter, L. (1954). Further notes on the swift, *Apus apus* L., as a predator of flies (Diptera). *Ent. Mon. Mag.* **90**, 230–231.

Three meals collected from swifts at Oxford after a period of rain and wind comprised 150 Diptera, 157 Hymenoptera, 237 Hemiptera, 70 Coleoptera, 87 unidentified insects and 5 spiders. The dipterous species represented are listed. Syrphids, among which females predominated, were the most numerous, and it is suggested that the birds fed in a area of sunshine, possibly approaching Oxford. Female syrphids usually fly nearer the ground than males.

Parmenter, L. (1955). Flies visiting the bluebell *Endymion nonscriptus* (L.) Garcke. *Ent. Rec.* **67**, 89–91.

A list of twelve species observed at bluebells with, in some cases, other flowers visited by them.

Thomas, D. C. (1955). Notes on the biology of some Hemiptera Heteroptera. II.—Coreoidea. *Entomologist*, **88**, 33–36.

Information on food plants, seasonal history, habitats and abundance of three coreids, an alydid, and two rhopalids in Devon and Cornwall.

Woodroffe, G. E. (1954). A note on the food-plants of *Berytinus minor* (Herr.-Sch.) and *B. signoreti* (Fieb.) (Hem., Coreidae). *Ent. Mon. Mag.* **90**, 175.

Trifolium repens is shown to be the food-plant of *B. minor* and *Lotus corniculatus* that of *B. signoreti*.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Allen, A. A. (1954). *Hypocoelus procerulus* Mannh. (Col., Eucnemidae, Anelastini) in Kent and Surrey: a tribe, genus and species new to Britain. *Ent. Mon. Mag.* **90**, 228–230.

Allen, A. A. (1954). *Bolitochara mulsanti* Sharp (Col., Staphylinidae) in Herefordshire and a critical note. *Ent. Mon. Mag.* **90**, 237.

Allen, A. A. (1954). *Bolitochara* spp. (Col., Staphylinidae): a correction. *Ent. Mon. Mag.* **90**, 302.

A new county record. Includes characters separating *B. mulsanti* from the other British species.

Allen, A. A. (1955). Notes on some Longicornia from Herefordshire. *Ent. Rec.* **67**, 88–89.

Includes two new county records.

Bagenal, T. B. (1954). *Ophiocten scutatum* Koehler at St Kilda. *Ann. Mag. Nat. Hist.* (12) **7**, 143–144.

Record of this brittle-star, only twice previously recorded in British seas.

Barnes, H. F. (1954). A new species of *Trotteria* Kieffer (Cecidomyidae) reared from unopened flower-buds of privet (*Ligustrum vulgare* L.). *Ent. Rec.* **66**, 281–283.

The new species is *T. ligustri*, the larvae of which are sometimes associated with those of *Placochela ligustri*.

Baynes, E. S. A. (1955). Migration of the dragonfly *Sympetrum danae* Sulzer. *Irish Nat. J.* **11**, 255.

Numbers seen flying north-west at Tory Island, Donegal, 6 September 1954.

Birkett, N. L. (1954). Some Cardiganshire Lepidoptera records 1954. *Ent. Rec.* **66**, 244–245.

Includes 23 species not hitherto recorded from Cardiganshire.

Boase, H. (1952). Mallard counts in the Tay Estuary and in Angus. *Brit. Birds*, **45**, 377–386.

Records of the number of *Anas platyrhyncha* on the Tay Estuary were made at all times of the year during 1914–25, and 1937–50, and, for comparison, from fresh water on Lintrathen Loch 1934–42, and 1945–50. These are plotted on graphs. On the estuary, no count exceeded 400 in the first period, but in the second ten have exceeded 1000, and the highest was 1800.

Boase, H. (1954). Movements and numbers of Tufted Duck in E. Scotland. *Brit. Birds*, **47**, 65–76.

The study is the result of frequent counts of the number of *Aythya fuligula* present on tidal water of the Tay Estuary, and on certain lochs in Angus and east Perthshire, during the periods 1912–27 and 1937–50. The sex ratios at different seasons are discussed.

Brindle, A. (1953). Diptera of the Pendle Hill Area. II. Tipulidae, Trichoceridae, Anisopodidae and Ptychopteridae. *Northw. Nat.* (N.S.) **1**, 55–65.

An annotated list for an area of mid-Lancashire.

Brown, P. E. (1953). The island of avocets. *Countryside* (N.S.), **16**, 377–380.

Bird visitors to Havergate Island.

Campbell, J. L. (1954). The Macrolepidoptera of the Isle of Canna. *Scot. Nat.* **66**, 101–121.

A list of fourteen butterflies and 176 moths taken since 1938.

Collingwood, C. A. (1955). Ants in S.W. Scotland. *Ent. Rec.* **67**, 11–12.

Includes four new county records for Ayrshire and one for Wigtownshire, with lists of the species of *Formica*, *Lasius* and *Myrmica* known from the two counties Kirkcudbrightshire and Dumfriesshire.

Conder, P. J. (1953). A list of the birds of Skokholm, Pembrokeshire. *Northw. Nat.* (N.S.) **1**, 211–219.

An annotated list.

Cooke, J. A. L. (1954). Some additions to the county records of spiders. *Ent. Mon. Mag.* **90**, 252–253.

A considerable number of new records for Salop, Hants, Notts, Norfolk, Oxon., Berks, Denbighshire, Montgomeryshire and Banffshire.

Cornwallis, R. K. (1954). Bird migration and population. *Trans. Lincs. Nat. Union*, **13**, 145–174.

A review of various aspects of bird migration in relation to population studies, with special reference to migrants through the British Isles.

Cramp, S. & Teagle, W. G. (1952). The birds of Inner London, 1900–1950. *Brit. Birds*, **45**, 433–456.

The paper consists mainly of a systematic list, but the probable causes of increases and decreases are discussed, and the ecological significance of changes in environments is briefly assessed.

Cuthbertson, E. I., Foggitt, G. T. & Tyler, G. E. (1954). Census of Swallows in the Sedbergh area, N.W. Yorkshire, in 1953. *Brit. Birds*, **47**, 204–205.

Comparison with three previous years is made. Special attention was paid to the siting and construction of nests, and hatching and fledging. A total of 166 nests were found, and much detail is condensed into two pages by the use of simple tables.

Davidson, W. F. (1954). *Plusia confusa* Steph., *Apamea ophiogramma* Esp. and *Cirrhia gilvago* Schiff. in Cumberland. *Ent. Rec.* **66**, 272–273.

C. gilvago is recorded for the first time from Cumberland, where it appears to be not uncommon.

Davies, H. (1954). On the occurrence in England of the earthworm *Allolobophora arnoldi* Gates, 1952. *Ann. Mag. Nat. Hist.* (12) **7**, 351–352.

Description. Habitat recorded.

Davies, L. (1954). *Prosimulium hirtipes* Fries (Dipt. Simuliidae) in England and Wales. *Ent. Mon. Mag.* **90**, 253.

This simuliid, which is widespread in the Scottish Highlands, is recorded from Westmorland, Cumberland and Caernarvonshire for the first time.

Davis, R. A. (1955). Occurrence of the Black Rat in sewers in Britain. *Nature, Lond.* **175**, 641.

Three locality records of *Rattus rattus*.

Donisthorpe, H. (1955). Coleoptera at Market Bosworth. *Ent. Rec.* **67**, 72.

Includes three species new to Leicestershire.

Duhig, M. & Humphries, C. (1955). *Amphilochus brunneus* Della Valle, an amphipod new to Britain and Ireland and notes on other amphipods not previously recorded in Irish coastal waters. *Proc. R. Irish Acad.* **57**(B), 123–129.

Records one new British amphipod and fifteen new to Ireland from littoral and off-shore waters, with some notes on habitats and rates of occurrence.

Edmondson, T. (1953). Some aspects of the natural history of Western Chat Moss. Birds, mammals and selected flowering plants. *Northw. Nat.* (N.S.) **1**, 400–416.

Chat Moss is a large raised bog which was largely drained in the nineteenth century. The list of birds includes useful ecological notes.

Fidler, J. H. (1953). The biology of some Yorkshire aphides. III. *Northw. Nat.* (N.S.) **1**, 220–226.

A list with ecological notes.

Ford, W. K. (1953). Lancashire and Cheshire Odonata (A preliminary list). *Northw. Nat.* (N.S.) **1**, 227–233.

An annotated list.

Galliford, A. L. (1953). Notes on the distribution and ecology of the Rotifera and Cladocera of North Wales. *Northw. Nat.* (N.S.) **1**, 513–529.

A list with stations, and a few ecological notes.

Gardiner, B. O. C. (1954). Some new Cambridgeshire Lepidoptera. *Ent. Rec.* **66**, 276.

Contains three new county records.

Gibson, J. A. (1953). Observations on the breeding birds of Ailsa Craig in 1947. *Northw. Nat.* (N.S.) **1**, 18–22.

A list with annotations. Eighteen species nested. There were 5383 pairs of Gannets (*Sula bassana*), compared with 4829 in 1942.

Grensted, L. W. (1954). *Psychoda surcoufi* Tonn. and *P. gemina* Eaton (Dipt., Psychodidae) in Oxfordshire. *Ent. Mon. Mag.* **90**, 189–190.

Both are new records for the county.

Harper, G. W. (1955). The Macrolepidoptera of Inverness-shire—Newtonmore district. Supplement No. 1. *Ent. Rec.* **67**, 39–40.

Includes several records new to the district [see 1954, *Ent. Rec.* **66**, 58–64, 90–9, 124–8 and abstract in 1954, *J. Anim. Ecol.* **23**, 395].

Hebditch, G. A. (1952). B.E.N.A. autumn migration enquiry. *Countryside* (N.S.) **16**, 271–272.

Small numbers of sky-larks were observed in 1951 and the movements of chaffinches in S. England were on a reduced scale.

Hebditch, G. A. (1953). B.E.N.A. autumn migration enquiry. *Countryside* (N.S.) **16**, 429–430.

High level flight of chaffinches and sky-larks.

Hewson, R. (1953). An apparently isolated colony of the Scottish Field Vole—*Microtus agrestis neglectus* Jenyns. *Northw. Nat.* (N.S.) **1**, 174–176.

At 2410 ft in Ross-shire, apparently isolated from other colonies by about half a mile, and surviving through snow for several months.

Kettle, D. S. & Lawson, J. W. H. (1955). Descriptions of two species of *Culicoides* Latreille (Diptera: Ceratopogonidae) new to science. *Proc. R. Ent. Soc. Lond.* (B) **24**, 37–47.

Records *Culicoides achrayi* n.sp. from Perthshire: Loch Achray, Trossachs and *Culicoides duddingstoni* n.sp. from Midlothian: Duddingston Loch, Edinburgh. Includes alterations to existing keys to the British *Culicoides* to accommodate the new species. Keys affected are Edwards (1939)—females, and the larval and pupal keys of Kettle and Lawson (1952).

Kettlewell, H. B. D. (1954). *Hydraecia hucherardi* Mabille (Lep., Agrotidae) breeding in Britain. *Entomologist*, **87**, 249–257.

This Noctuid, till recently known only from France, was found breeding in *Althaea officinalis* in Romney Marsh in 1954 and may be indigenous in other localities where this plant occurs, a list of which is given.

Le Quesne, W. J. (1954). Some new county records of Hemiptera Heteroptera. *Ent. Mon. Mag.* **90**, 250.

A large number of new records for Bucks, Middlesex, Berks, Oxon., Yorks, Westmorland and Ireland.

Le Quesne, W. J. (1954). *Zygina rubrovittata* Leth. (Hem., Cicadellidae) from two additional British counties. *Ent. Mon. Mag.* **90**, 303.

This species is recorded for the first time from Buckinghamshire and Hampshire, in both of which it was associated with *Calluna*.

Leutscher, A. (1954). The edible dormouse in Britain. *Discovery*, **15**, 70–71.

The present distribution of *Glis glis* is a triangle bordered at the corners by the towns of Beaconsfield, Aylesbury and Luton, with Tring as the centre of irruption.

Lloyd, R. W. (1954). *Plectophloeus nitidus* Fairmaire (Col., Pselaphidae) in Oxfordshire. *Ent. Mon. Mag.* **90**, 189.

This beetle was hitherto known only from Herefordshire and Berkshire.

Long, A. G. (1954). Some Berwickshire Lepidoptera records, 1952–54. *Ent. Rec.* **66**, 284–287.

Includes several new county records.

Longstaff, T. G. (1954). Migration along the north-west coast of Scotland. *Scot. Nat.* **66**, 94–100.

Notes on migrant birds made at Achiltibuie, Ross-shire, since 1942.

Macan, T. T. & Lund, J. W. G. (1954). Records from some Irish Lakes. Part 1. Mollusca, *Gammarus*, *Asellus*, Ephemeroptera, and Heteroptera. Part 2. Phytoplankton. *Proc. R. Irish Acad.* **56B**, 135–157.

Thirty-three stations, with information on pH, $Ca^{\cdot\cdot}$, conductivity, nature of bottom, and macrophytic vegetation.

MacEwen, E. A. T. & Hobson, A. D. (1954). Occurrence of *Paracentrotus lividus* (Lamarck) in Scotland. *Nature, Lond.* **174**, 752.

Records this sea-urchin from the inter-tidal zone of the Isle of Muck, Inverness-shire, in 1939.

McRitchie, J. A. (1952). The arrival of spring migrants, 1951. *Countryside* (N.S.), **16**, 191–193.

McRitchie, J. A. (1953). The arrival of spring migrants, 1952. *Countryside* (N.S.), **16**, 343–346.

McRitchie, J. A. (1954). The arrival of spring migrants, 1953. *Countryside* (N.S.), **17**, 15–18.

Marchant, S. (1952). The status of the Black-headed Gull colony at Ravenglass. *Brit. Birds*, **45**, 22–27.

The population was overestimated when a survey of *Larus ridibundus* colonies in Britain was made in 1938, and the revised estimate of population at that time is reduced to about 10 000 breeding pairs, instead of 'some tens of thousands'. A decrease has since occurred, and in 1951 the figure is given as 5000–5500. It is shown on what data the estimates are based.

Matthews, L. H. (1954). The migration of mammals. *Discovery*, **15**, 202–206.

An account of migration with especial reference to lemmings and bats.

Michaelis, H. N. (1955). Microlepidoptera in Cheshire and South Lancashire in 1953–54. *Ent. Rec.* **67**, 12–14.

Includes seven new records for Cheshire.

Mistakidis, M. N. & Hancock, D. A. (1955). Reappearance of *Ocenebra erinacea* (L.) off the east coast of England. *Nature, Lond.* **175**, 734.

Morton, J. E. & Holme, N. A. (1955). The occurrence at Plymouth of the opisthobranch *Akera bullata*, with notes on its habits and relationships. *J. Mar. Biol. Ass. U.K.* **34**, 101–112.

First record of this mollusc from Plymouth. The characteristic swimming movements and the structure of the digestive system are described.

Newman, L. H. (1955). *Nymphalis antiopa*: migrant or stowaway? *Entomologist*, **88**, 25–27.

The author presents evidence supporting the view that *N. antiopa* reaches Britain in ships, mainly from Norway, Sweden, Denmark and Finland, carrying timber in which it has sought hibernation quarters, and not as a migrant.

Peacey, A. F. (1954). *Leioptilus carphodactylus* Hübn. and *Platyptilia isodactyla* Zell. in Gloucestershire (v.c. 33). *Ent. Rec.* **66**, 260–261.

L. carphodactylus is recorded from Gloucestershire, where it was breeding on limestone, for the first time; it was hitherto known only on chalk.

Pearce, E. J. (1954). *Bryaxis laminatus* Mots. (Col., Pselpahidae): an addition to the British list. *Ent. Mon. Mag.* **90**, 202–203.

Pearce, E. J. (1954). New aquatic Coleoptera records for Herefordshire. *Ent. Mon. Mag.* **90**, 247.

Contains six new county records.

Powell, H. T. (1954). Occurrence of *Chthamalus stellatus* (Poli) in Fair Isle and Shetland. *Nature, Lond.* **173**, 688.

Most northerly record of this barnacle. Its limited distribution in the British Isles suggests that hydrographic as well as temperature conditions affect its distribution.

Ragge, D. R. (1954). The distribution of *Chorthippus vagans* (Eversmann) in Dorset and Hampshire (Orth., Acrididae). *Entomologist*, **87**, 230–231.

Includes a couplet separating this species from *C. brunneus* and some ecological data.

Smith, A. E. & Cornwallis, R. K. (1955). The birds of Lincolnshire. *Lincolnshire Natural History Brochure* No. **2**. (Lincolnshire Naturalists' Union, Lincoln, 136 pp.)

A new check-list of the birds of the county, with three good introductory chapters on the effect of land use on the avifauna, migration, and the history of the study of birds in Lincolnshire.

Smith, K. G. V. (1954). Breeding records of two British Muscidae (Dipt.). *Ent. Mon. Mag.* **90**, 222.

Helina duplicata emerged from larvae under moss and *Eustalomyia histrio* from a pupa in a living cherry trunk, both in Shropshire.

Snow, D. W. (1953). Visible migration in the British Isles: a review. *Ibis*, **95**, 242–270.

The chief observations on visible migration in the British Isles are brought together, differences in behaviour of different species are mentioned, and attention is drawn to gaps in our knowledge.

Snow, D. W. (1953). The migration of the Greenland Wheatear. *Ibis*, **95**, 376–378.

From an examination of the literature of ocean voyages it is concluded that *Oenanthe o. leucorrhea* undertakes the longest regular trans-ocean migration of any passerine bird, the tendency being for overland travel with short sea crossings to be more usual in spring.

Southward, A. J. & Crisp, D. J. (1954). The distribution of certain intertidal animals around the Irish coast. *Proc. R. Irish Acad.* **57B**, 1–29.

Ten species (2 barnacles, 1 isopod, 6 gastropods, 1 echinoid), 96 stations. Population densities and correlations with the environment.

Southwood, E. C. (1955). Polychaeta new to the British Isles. *Nature, Lond.* **175**, 264.

List of Polychaeta new to British Isles, and seventy species new to Irish Sea.

Stratton, L. W. (1955). The Mollusca of Hertfordshire. *Trans. Herts. Nat. Hist. Soc.* **24**, 81–118.

A faunistic list with occasional brief notes on habitat. Several species have been introduced from time to time.

Taylor, M. (1954). Distribution of *Pelmatohydra oligactis* (Pallas) in Scotland. *Nature, Lond.* **175**, 44–45.

Circumstantial evidence suggests this species has spread to Scotland.

Thomson, A. L. (1953). The study of the visible migration of birds: an introductory review. *Ibis*, **95**, 165–180.

A summary of the main conclusions to be drawn from a series of papers on visible migration in western and central Europe and the Mediterranean region.

Tucker, D. W. (1955). The Long-finned Tunny, *Germo alalunga* (Bonnaterre), in British seas. *Nature, Lond.* **175**, 174.

Relation to studies on effects of climatic fluctuations on distribution of northern faunas.

Wakely, S. (1954). Occurrence of *Coleophora clypeiferella* Hofmann in England. *Ent. Rec.* **66**, 272.

This record, from Camberwell, is the first for this species in Britain.

Watson, A. (1954). Curlew nesting in cornfields. *Scot. Nat.* **66**, 125.

A census of the nesting sites of 113 pairs of curlew in the Turriff district of Aberdeenshire and Banffshire in 1945.

Williams, T. S. (1954). Further observations on sheld-duck on the Welsh side of the Dee estuary. *Proc. Liverpool Nat. Fld. Cl.* **1953**, 21.

Observations on numbers of *Tadorna tadorna* seen in 1953.

Williamson, M. H. (1954). *Chernes cimicoides* (F.) (Pseudoscorp.) in a nest of *Lasius brunneus* (Latr.) (Hym., Formicidae). *Ent. Mon. Mag.* **90**, 172.

C. cimicoides has several times been recorded under bark in Oxfordshire, but this record for the same county is apparently the first from nests of *L. brunneus*.

Wilson, D. P. (1953). Foreign animals on British shores. *Discovery*, **14**, 206–209.

Discusses *Physalia, Velella, Lampris luna* and *Caretta caretta.*

Woodroffe, G. E. (1955). The Hemiptera-Heteroptera of some cinder-covered waste land at Slough, Buckinghamshire. *Ent. Rec.* **88**, 10–17.

An annotated list of twenty coreids, neidids, lygaeids, tingids, nabids, mirids and saldids for which the habitat seemed particularly favourable, with ecological data.

Yarrow, I. H. H. (1954). *Formica exsecta* Nylander (Hym., Formicidae) in the British Isles. *Ent. Mon. Mag.* **90**, 183–185.

A review of the distribution, with a map.

6. STUDIES ON BEHAVIOUR

Allison, F. R. (1952). Reactions of Fulmars to Skuas. *Brit. Birds*, **45**, 35.

Fulmarus glacialis was observed to display aggressively when approached by a *Stercorarius parasiticus*, and more intensely when near *Stercorarius skua* sitting on the water.

Armstrong, E. A. (1952). The distraction displays of the Little Ringed Plover and territorial competition with the Ringed Plover. *Brit. Birds*, **45**, 55–59.

Three forms of distraction display by a pair of *Charadrius dubius* with chicks are described, and territorial quarrels with a *Charadrius hiaticula*. Both species bred successfully.

Barnett, S. A. (1955). Competition among wild rats. *Nature, Lond.* **175**, 126–127.

Fighting amongst captive males due to competitive behaviour. Also inter-specific competition between *Rattus rattus* and *R. norvegicus*. Densely populated male-female colonies show high mortality amongst males and in litters. Controls do not show this. The filmed behaviour of marked animals is related to physiological differences noticed at autopsy, particularly in the adrenals. Indicates competition is evoked by a number of specific situations.

Chettleburgh, M. R. (1952). Observations on the collection and burial of acorns by Jays in Hainault Forest. *Brit. Birds*, **45**, 359–364.

When collection was at its peak during 10 days in mid-October, the whole population of *Garrulus glandarius* in the forest appeared to be engaged in the collection and burial of acorns throughout the day, and they were buried up to three-quarters of a mile from the collection area. It is estimated that for the whole period 200 000 acorns were buried.

Corbet, P. S. (1955). A critical response to changing length of day in an insect. *Nature, Lond.* **175**, 338–339.

Anax imperator emerges as two distinct groups, which have overwintered as final and penultimate instars respectively. Diapause facultative, hence larvae entering final instar in spring need not postpone emergence another year. Strict seasonal incidence of diapause suggests that causative factor is changing day length. Preliminary experiments tend to support this. A similar response may be found in species which have a larval duration of more than one year, i.e. to changing rather than absolute day length.

Goodwin, D. (1952). Notes and display of the Magpie. *Brit. Birds*, **45**, 113–122.

Based on observations of both wild and captive birds. The principal notes and their significance are described. The displays are illustrated with text figures.

Haine, E. (1955). Aphid take-off in controlled wind speeds. *Nature, Lond.* **175**, 474–475.

Twenty species, host alternating and non-alternating, are considered, together with their seasonal forms. Differences in the behaviour of these are shown. In tunnel experiments wind speed is isolated from other factors, its influence being over-riding.

Harker, J. E. (1955). Control of diurnal rhythms of activity in *Periplaneta americana* L. *Nature, Lond.* **175**, 733.

Implantation of suboesophageal ganglia into headless cockroaches causes the activity rhythm to be close to that of the donor. Ocelli are suggested as the overall timekeepers, as there is no true diurnal rhythm. Implantation of ganglia from normal insects into intact cockroaches which have lost rhythm causes rhythm to be regained. If donor and recipient have same rhythm, there is no change but the level of activity in dark period is depressed.

Hinde, R. A. (1953). A possible explanation of paper-tearing behaviour in birds. *Brit. Birds*, **46**, 21–23.

It is suggested that paper-tearing is an expression of the hunting drive, which is not restricted to times when birds are hungry.

Home, W. M. Logan (1953). Paper-tearing by birds. *Brit. Birds*, **46**, 16–21.

Data were obtained from about 2250 observers, and these are briefly summarized. *Parus* spp. are the only group of birds in which the habit is common, and its significance remains obscure, but hunger is not a cause. It occurs chiefly in autumn, and the evidence suggests that dry weather promotes it.

Jackson, R. D. (1952). The display of the Blackbird. *Brit. Birds*, **45**, 103–104.

Observations on four pairs of *Turdus merula* over two seasons, and on a fifth pair in the second year. Courtship and threat displays are described, and the necessity for the identity of the birds being known for an accurate account to be given is stressed.

Jackson, R. D. (1954). Territory and pair-formation in the Blackbird. *Brit. Birds*, **47**, 123–131.

A study of a suburban population of about four pairs of *Turdus merula* on an area of 5½ acres from 1948 to 1953.

Kramer, G. (1952). Experiments on bird orientation. *Ibis*, **94**, 265–285.

Captive *Sturnus vulgaris* and homing pigeons were used. The former tended towards the south-west in autumn. Both could be trained to choose food from a definite direction. Pigeons on release appear to be orientated before starting, and sun-navigation is the probable explanation, but other orientation mechanisms may be involved, as sun-orientation is not a satisfactory hypothesis by night.

Lack, D. & Lack, E. (1952). The breeding behaviour of the Swift. *Brit. Birds*, **45**, 186–215.

A study of the behaviour of *Apus apus* at the nest. A colony at Oxford was induced to use nest boxes with glass backs.

Marler, P. (1952). Variation in the song of the Chaffinch *Fringilla coelebs*. *Ibis*, **94**, 458–472.

A method for transcribing the song is described. Songs from five localities, three in Britain, one in France, and one in the Azores, are compared, and it is shown statistically that geographical variation occurs. The existence of song types exclusive to a particular region cannot be substantiated. The phenotypic nature of the song leads to the conclusion that its geographical variation should not be regarded as an example of incipient speciation.

Matthews, G. V. T. (1952). An investigation of homing ability in two species of gulls. *Ibis*, **94**, 243–264.

Homing experiments in which 249 *Larus fuscus graellsii* and 91 *Larus a. argentatus* were used are described. The migratory *L. fuscus* on release showed a significant homeward orientation when the sun was not obscured by clouds, and their overall performance was better than that of *L. argentatus*. The majority of the gulls homed by an inefficient method, probably random exploration for landmarks, but a minority were homing by a method not dependent on the distance or area of release, a form of sun navigation being suggested. Magnets attached to birds to mask the earth's magnetic field did not affect homing ability.

Matthews, G. V. T. (1953). Direction finding in birds. *Discovery*, **14**, 145–150.

A review of recent work on sun navigation.

Pirenne, M. H. & Marriott, F. H. C. (1955). Light sensitivity in the flatworm *Dendrocoelum lacteum*. *Nature, Lond.* **175**, 642.

Response by movement to various visible and near ultra-violet spectral bands. Sensitivity curve of flatworm found to be roughly similar to that of rod vision in human aphakic eye, except at the violet end of the spectrum.

Qasim, S. Z. (1955). Rearing experiments on marine teleosts and evidence of their need for sleep. *Nature, Lond.* **175**, 217–218.

Rearing in the laboratory. Investigation of the nutritional value of phytoplankton cultures, and nauplii, to *Centronotus gunnellus* and *Blennius pholis*. The latter has functional swim bladder in the larval stages. Larvae under alternating light and dark showed periods of inactivity (sleep), and a greater survival rate.

Radford, M. C. (1954). Notes on the winter roosting and behaviour of a pair of Nuthatches. *Brit. Birds*, **47**, 166–168.

A female *Sitta europea* was observed going to roost and rising daily from October to March. Light appeared more important than temperature in determining the time of rising. Roosting was less regular, and tended to be late in cold weather.

Ribbands, C. R. (1955). Communication between honeybees: II. The recruitment of trained bees, and their response to improvement of the crop. *Proc. R. Ent. Soc. Lond.* (A) **30**, 26–32.

Experiments with individually marked bees have shown that at a source where the supply is improved the number of recruits is doubled. Individual differences were marked. The implications of the results are discussed with relation to dancing, scenting and recruiting and the circumstances in which recruiting occurs.

Ribbands, R. (1955). The scent language of honeybees. *Discovery*, **16**, 22–23, 25–26.

Indications of current research into bee recognition by scent, and into food sharing within the colony. Strong evidence has been accumulated to indicate that food sharing is the basis of communication in the colony.

Sage, B. L. (1955). A mass emergence of the dragonfly, *Ischnura elegans*. *Entomologist*, **88**, 20–21.

At least 200 individuals were involved in this mass emergence in Carmarthenshire.

Summers-Smith, D. (1954). Colonial behaviour in the House Sparrow. *Brit. Birds*, **47**, 249–265.

Observations on the *Passer domesticus* population of two square miles in Hampshire. It is shown that they tend to form colonies isolated from each other. The structure of one colony in which the birds were colour-ringed was studied in detail.

Tinbergen, N. (1952). On the significance of territory in the Herring Gull. *Ibis*, **94**, 158–159.

It is suggested that the territorial system of *Larus argentatus* is a defence against predators by spreading out the cryptically coloured eggs and young.

Tinbergen, N. (1952). A note on the origin and evolution of threat display. *Ibis*, **94**, 160–162.

Threat display is attributed to a balanced condition of the fighting and escape drives, and results in the avoidance of much fighting. As the fighting drive plays a part in courtship, an evolutionary increase in its strength would disturb mating.

Tinbergen, N. & Moynihan, M. (1952). Head flagging in the Blackheaded Gull; its function and origin. *Brit. Birds*, **45**, 19–22.

The courtship of *Larus ridibundus* is described, and it is pointed out that contrary to reports in the literature, pair formation often takes place in or near breeding colonies on 'pre-territories' taken up by single males. Head flagging is an appeasement gesture of which the function seems to be to nullify threatening gestures, and conspicuous structures are concealed rather than displayed.

Williamson, K. (1952). Regional variation in the distraction displays of the Oystercatcher. *Ibis*, **94**, 85–96.

Five types of distraction display of *Haematopus ostralegus* are described, and their regional importance is commented on. Three of them are more highly developed in the Faeroe Islands, where an atypical moorland habitat has been colonized in comparatively recent times, than elsewhere. Their evolution is attributed to frequent disturbance of the brooding urge by man in the absence of other terrestrial predators except dogs.

7. REPORTS OF ORGANIZATIONS

Lundy Field Society (1955). Eighth Annual Report, 1954. (Hon. Secretary, University College, Exeter, 2*s.* 6*d.*; 46 pp.)

In addition to the usual faunistic lists of birds (with notes on appearance and behaviour, visible migration and ringing) and mammals, there are contributions on recoveries of ringed shags, the census of nesting sea-birds and bird ectoparasites.

Directors' Report for 1952 (1953). *Rep. Mar. Biol. Sta. Pt Erin*, **65**, 7–23.

Ecological work being done at the Station included observations on herring, norway pout, inshore populations of young fish, and scallops. Local water-masses and water-movements have been investigated chemically and by means of the Hardy plankton indicator. Among observations on bottom faunas, work was in progress on the inter-relationships between species living in muddy sand, on the local polychaete fauna, and on the effects of climate on inter-tidal animals.

Directors' Report for 1953 (1954). *Rep. Mar. Biol. Sta. Pt Erin*, **66**, 5–16.

Ecological work in progress at the station included further observations on herrings and their young, and young fish both off-shore and inshore. Work on scallops was completed, and investigations into the growth, breeding and ecology of the queen scallop, *Chlamys opercularis*, begun.

Work continued on the local population of Polychaets, Phoronids and Enteropneusts, Isopods and Pagurids. The watermasses in the surrounding seas were again investigated both chemically and biologically.

Surrey Bird Report for 1953. (Haslemere Educational Museum, Haslemere, Surrey, 2*s.*, pp. 16; 1954.)

A new county bird report, which besides the usual faunistic data has short notes on winter movements of rooks, jackdaws, starlings and black-headed gulls, and on the feeding behaviour of birds at a sewage farm.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING IN LONDON

2–3 April 1954

At Easter the Society again enjoyed the hospitality of Professor W. H. Pearsall at the Department of Botany, University College, Gower Street, London. The meeting was well attended, 85 members being present.

2 *April*. The morning session commenced at 10.30 a.m. with Prof. A. R. Clapham, the President of the Society, in the Chair. The first paper was given by Dr Eville Gorham 'On the ionic composition of fen and bog waters, considered in relation to habitat and vegetation'. Dr Gorham outlined the study he had made of Ca, Na, K, KCO_3, pH and specific conductivity in fen and bog waters from three peaty Lake District sites: Esthwaite North Fen, Dale Park Moss and Rusland Moss. Except for the richest Esthwaite samples, the waters possess a lower proportion of Ca and a higher proportion of Na than the average fresh water of the world. The explanation is presumably that in these waters there is a lesser influence of Ca leaching from the surrounding mineral soils, so that the Na supplied by sea spray (*via* rain) is of greater importance than normally.

Esthwaite Fen shows the highest levels of Ca and HCO_3. Dale Park Moss is intermediate, and Rusland Moss is lowest, with HCO_3 entirely absent. This is in line with the vegetational differences, the Esthwaite communities being reedswamp, grass-sedge meadow and alder-willow carr; those at Dale Park *Sphagnum*-sedge lacustrine bog; and the Rusland vegetation typical of dry raised bog, with pinewood, cotton-grass-heather, and *Sphagnum*-dominated areas. At Esthwaite the waters are circum-neutral, and Ca exceeds Na except in a sample from a *Sphagnum* patch. At Rusland the waters are strongly acid, and Na exceeds Ca. Na and K are much the same in all three sites, the latter being least plentiful of the three metal cations, and varying irregularly in concentration.

The actual concentrations of cations in the waters are very much less than the potential concentrations, if the cations adsorbed on the peat colloids could be displaced into solution. This is true of both metal cations and hydrogen ions. The question arises as to how efficiently plants can utilize the adsorbed metal cations, especially from bog peats whose adsorptive capacity may be saturated by hydrogen ions to the extent of 75–95%.

Rusland Moss waters show higher levels of Ca, Na and K than waters from Swedish raised bogs. This may explain the presence on British raised bogs of *Eriophorum angustifolium* and *Narthecium ossifragum*, which in Sweden are absent from the raised bog surfaces though often present in the flushed marginal laggs.

In the discussion that followed considerable interest was shown in the high sodium content of the fen and bog waters studied. Prof. Clapham, H. C. Gilson, F. H. Perring, P. J. Newbould, and Dr R. E. Hughes took part in the discussion.

Prof. W. H. Pearsall then gave his paper on 'The bog surface as a dynamic system'. Prof. Pearsall questioned the role of the 'regeneration complex' of Osvald in bog growth. Undulations in bogs, giving rise to raised areas which may simulate 'a regeneration complex' could be developed in two ways: either by movement of peat or due to shrinkage of the peat mass. Professor Pearsall's stimulating remarks were supported by excellent illustrations of Swedish bogs.

Prof. Pearsall's views were criticized by Dr H. Godwin: while he admitted that movement and contraction of peat could play an important role in the production of undulations on bog surfaces, the 'movement' mechanism could only be applicable to bogs on slopes—and not to those on flat ground such as occurred in Ireland. Dr Godwin considered that the 'regeneration complex' did occur and contributed to bog growth.

It was also pointed out that in Sweden there was a more pronounced seasonal variation in water levels in the bogs.

Dr Conway pointed out that in Tregaron regeneration of bog did occur on burnt surfaces.

Several other members of the Society took part in a very interesting and controversial discussion. These included Professor Clapham, Dr Murphy, P. J. Newbould, Dr Gorham and Dr Boatman.

The last paper of the morning session was given by Dr A. J. Rutter, this being on 'Variation in the structure of a wet heath community in relation to the water-table'.

The range of closely related communities dealt with is characteristic of the wet-heaths of S.E. England. The central associes is dominated by *Molinia* and *Calluna*, with *Erica tetralix* usually very abundant. The surface soil consists of tussocks formed by the accumulation of dead shoot bases and roots of *Molinia*. All three plants root freely in this tussock horizon and the roots of *Calluna* are largely restricted to it.

Under varying conditions any one of these plants may increase in importance relative to the others. When conditions are near to those of Valley Bog, *Erica* is particularly important. Elsewhere *Molinia* assumes complete dominance. There is a wet type of Molinietum, characterized by marked tussock building, and a drier type with only moderate tussock building, the two grading into one another. Increase of *Calluna* occurs in transitions between wet- and dry-heaths, and is accompanied by more rapid tussock decomposition.

A statistical study of the relation between botanical composition and water-table depth, showed that it was necessary to separate the apparent effects of tussock height, and depth of water-table below the soil surface (i.e. the soil excluding the tussock). The proportion of *Molinia* rose both with increasing tussock height and with falling water-table, and the behaviour of *Erica* was almost exactly the reverse of this. In both cases unit change in tussock height had greater apparent effect that unit change in water-table depth. *Calluna* also decreased in amount as tussock height increased, but was not affected by water-table depth. Alternatively, the proportion of *Molinia* could be closely related to water-table fluctuation, which was believed to be a reflection of ground water movement. Tussock height is probably determined by balance between the rates of *Molinia* growth and decomposition. Weight data from clipped quadrats showed the importance of competition between the species. It is difficult to distinguish in any species between the direct effect of environmental change and the indirect effects due to changes in the competitive power of other species. The main changes are, firstly, a decrease in *Erica* and a corresponding increase in *Molina* associated with increased water-table fluctuation; and secondly a decrease in *Calluna* associated with increase in tussock height which may be due as much to retarded decomposition in high tussocks as to increasing competition from *Molinia*.

In the discussion that followed Dr Godwin mentioned the part played by transpiration in the diurnal variation in the water-table. Prof. Clapham, Drs Ovington and Hughes and P. J. Newbould took part in the discussion.

The afternoon meeting was held at 2.0 p.m. The first paper was by R. D. Hughes on 'Sampling the population of a Chloropid fly, in relation to the micro-climate'.

Mr Hughes discussed an attempt to calculate a correction coefficient for the effect of weather conditions upon the size of the catch of insects taken by a sweepnet.

The existence of such a coefficient in a computable form depends on (i) the effect of each separate climatic factor being constant, and (ii) the effect of the combination of climatic factors must be the sum of their individual effects.

In the narrowed field of research represented by the populations of the Chloropid fly *Meromyza variegata* which occurs in large numbers among *Dactylis glomerata*, the effect of each separate climatic factor was demonstrated to be constant by simulating natural conditions in an observation chamber in the laboratory. Within this, the conditions of wind-speed, air temperature, light intensity and moisture could be varied.

The insect populations move vertically within the grass, being distributed about a level governed by the conditions of the micro-climate.

The apparent summing of the individual effects to give the combined effect can be explained by the different factors operating independently on individual insects in different micro-habitats, so that the total insect population seemed to respond to the combined effect.

It was necessary to define which factors were operating to alter the micro-climate which in turn causes the insects to move. The temperature micro-climate for example, is related to the solar radiation intensity, the penetration of the radiation into the grass layer, and to the wind-speed.

Heat gradient experiments showed that the insect preferred higher temperatures and it was shown that through their effects on the temperature micro-climate alone, both the wind-speed and the penetration of radiation would have negative correlations with the size of the catch.

Similar observations on all the micro-climatic gradients, together with some knowledge of the behaviour of the insect, showed that probable negative correlations exist between the catch size and the wind-speed, radiation intensity, penetration of radiation and the length of time since the last rainfall. A probable positive correlation also exists between the catch and the air temperature within the grass layer.

A sampling experiment, observing the numbers of flies caught under different prevailing weather conditions, enabled the simultaneous correlation of the size of the catch with all the five climatic factors given above. The regressions obtained from this complicated calculation account for about sixty percent of the variance of the sampling data from which they were obtained. An example of the use of the weather coefficient, as derived from graphical regression curves, showed that in practice such a coefficient could substantially alter the interpretation of data.

In the discussion that followed Mr J. G. Skellam, Dr Satchell, Captain Diver, Drs Gorham and Hughes. and E. D. Le Cren took part.

Miss E. M. Evans followed with a paper on 'Growth forms of Bryophytes in relation to successiona and environmental change'.

The ecology of bryophytes in two types of woodland (relict oakwood on Millstone Grit and mixed ashwood on Magnesian limestone), both near Sheffield, were studied in detail by Miss Evans. The epiphytic communities, and those on boulders, fallen logs and soil, have been described from the point of view of floristic composition and structure. Community structure was classified according to the growth form classification (suitably amended) proposed by Gimingham & Robertson (1950).

Available data indicates that diversity of growth form among bryophyte communities can be attributed to environmental and successional change.

(i) *Successional change.* A comparison of community structure within the succession observed on logs and boulders brings out the following points:

(*a*) Growth form succession on rocks and logs within the *same* wood is almost identical.

(*b*) On boulders in the two woodland types, there are only two growth form classes common to both.

(*c*) On all substrata there is a comparable increase in complexity of structure from pioneer to climax communities.

To assist in elucidation of (*b*), additional evidence from two Swedish woods was produced. This showed that although chemical nature of the substratum plays a large part in determining the specific composition, and therefore indirectly affects the growth form, community structure is ultimately determined by the micro-climate. From a study of the different succession, the growth form classes can be arranged in order of *complexity*:

Crustaceous mat → Thalloid mat → Short turf → Smooth mat → (lichens).
Rough mat → Tall turf → Spreading-branch weft → Dendroid.

(ii) *Environmental change.* Community structure is affected by:

(*a*) Physical nature of the substratum, i.e. slope and texture of surface. Texture affects ease of colonization and potential water supply. On a sloping surface, the force of gravity limits development. less water is available and rapid drainage is promoted.

(*b*) Micro-climate. Micro-climatic gradients between the ground and upper air layers are accompanied by a zonation of bryophyte communities of different structure. From a study of different zonations. the growth form classes can be arranged in *order of micro-climatic tolerance*, which is identical with the above-mentioned *order of complexity*.

The common factor in both environmental and successional change is water supply. On a vertical surface there is a stable relationship between structural zonation and gradients in micro-climate, chiefly saturation deficit. In the course of any plant succession, the water potential of both substratum and the lowest air layers is increased, enabling more mesophytic species to become established, until the climax, with the highest water potential, is attained. It is concluded that the amount of water in the substratum and atmosphere is the greatest single factor determining community structure

(Gimingham, C. H. & Robertson, E. T. (1950). 'Preliminary investigations on the structure of bryophytic communities, *Trans. Brit. Bryol. Soc.* **1** (4), 330–44.

This paper stimulated considerable discussion in which Drs A. S. Watt, Ovington, Gorham, Wanstall, Clark and Boatman, Captain Diver and Prof. A. R. Clapham and Prof. P. W. Richards took part. The various points discussed were:

1. The role of the exudation of water bringing with it nutrients in solution from the substrata.
2. The importance of water-supply and its variation, in different habitats, and with time, with particular reference to the alternation of dry and wet conditions.
3. The time sequences in the development of the climax communities were about 50 years.
4. The role of light intensity in the control of community structure.

The final paper of the day was given by Dr A. T. Clifford on the 'Quantitative study of a hybrid swarm in the genus *Eucalyptus*'.

When mapping the distribution of the species of Eucalyptus in the region of the Dandenong Range near Melbourne, Australia, it proved impossible to delimit the habitat requirements of *E. elaeophora* and *E. goniocalyx*. In a general way it could be said that *E. elaeophora* grew where the annual rainfall was less than about 35 inches, whereas *E. goniocalyx* grew in wetter areas. The difficulty in deciding the habitat requirements of the two species arose through their merging into one another on the hillsides, in this area.

That such a range of intermediate forms was not the result of the plasticity of a single species growing in a series of intermediate habitats, was fairly certain. Where *E. goniocalyx* has been grown in plantations in dry localities it retains its characteristic bark as well as its fruit characters. Similarly where *E. elaeophora* is grown under conditions of higher rainfall than 35 in. per annum, it shows no tendency to develop differently from the way that it does in its natural habitat.

The intergrading of the two species seemed to be the outcome of current or previous hybridization. This was suggested by the appearance of coppice shoots on the stools of felled trees. In the zone of intermediate forms the shape of leaves of comparable age on coppice shoots, differed from stool to stool. The leaf shape of coppice shoots is characteristic for both *E. elaeophora* and *E. goniocalyx*; the former has round leaves whereas those of the latter are ovate-lanceolate. In stools of either species growing at a distance from the other, the shape of comparable leaves on the coppice shoots is very uniform.

The seedling leaves of both species are similar to their coppice leaves, and so it was decided to use them to study the genetic constitution of certain stands. In these stands in which only *E. elaeophora* or *E. goniocalyx* is present the seedlings raised from any tree should be uniform. If the species is genetically homogeneous then either inbreeding or outbreeding will give uniform seedlings from a given tree. But if the members of a stand have suffered from hybridization the seed of any tree will show some segregation amongst its progeny. With inbreeding this segregation may be greater than with outbreeding. The degree of variability between seedlings from a single tree can therefore give some indication of the genetic constitution of the members of a stand.

Taking trees which gave uniform seedlings which are typical of their respective species, it was possible to describe each species in such a way as to exclude simple hybrids. Having redefined the definition of the species it was possible to map their distribution and to define their ecological requirements. In general it can be said that *E. elaeophora* grows on the inland slopes of the Eastern Highlands, whereas *E. goinocalyx* grows on their seaward slopes. But in Victoria the habitats of the two species meet and here hybridization has taken place. A knowledge of this is important not only for understanding the ecology of the species, but also their taxonomy, which has in the past been confused by the failure to recognize that the species not so much intergrade as hybridize.

In the discussion that followed Dr A. S. Watt, E. D. Le Cren, J. G. Skellam, Prof. Valentine, Dr Heslop Harrison, Prof. Pearsall, and Dr Bell took part. The main points that emerged in discussion were:

1. Pollination in relation to distance of insect travel.
2. The role of man's activities, leading to the disturbance of the natural distribution of the two species, and their ultimate hybridization.
3. No self-incompatibility was known.

At 8 p.m. on the evening of 2 April a soirée was held in the Department of Botany of University College. This meeting was well attended, and the Society spent a very enjoyable evening, again, through Prof. Pearsall's generous hospitality. At the soirée an interesting range of exhibits were set out which included those of D. H. Dalby illustrating his work on *Salicornia*, Dr Goodman on *Lunularia cruciata* in South Wales, Dr Clifford on Australian *Eucalyptus*, Dr Martin on features of a South African fen, Dr H. G. Baker on ecotype of *Adoxa moschatellina*, and finally illustrations of the East Anglian floods of 1953.

3 *April*. The morning session opened at 10.30 a.m. with a paper by Prof. P. W. Richards on 'Botanical impressions of Spain during the tenth International Phytosociological Excursion'. This excursion was held in Spain from 25 June to 22 July 1953 and attended by twenty-six botanists from eleven different countries. The excursion was in two parts, the first starting from Barcelona and reaching Madrid via Saragossa, the Pyrenees, the Asturas, Valicia and Salamanca, the second being a trip to Cordoba and the Sierra Nevada and back from Madrid. Among the outstanding impressions were the sharp contrast in environment and in vegetation between the relatively moist north-western Spain, and the dry regions elsewhere, and also the extreme richness of the flora. In many parts of Spain primitive agricultural practices survive, including, in Valencia an interesting system in which crops of *Ulex europaeus* and *Sarothamnus welwitschii* form part of the rotation. The paper was illustrated by colour photographs.

In the ensuing discussion Prof. Clapham, Drs Godwin, Watt and Hughes took part. The use, within living memory, of *Ulex europaeus* in farm rotation in western Britain was referred to. It apparently reached Wales by the sixteenth century, when it was known as French Gorse. Prof. W. H. Pearsall then followed with a brief illustrated account of his visit to East Africa.

The next paper was given by J. Brereton on the 'Factors controlling *Tribolium confusum* populations'. A preliminary analysis of a study of the initial growth of *Tribolium confusum* was presented. The analysis showed that during the first 200 days of growth of the population, there appeared to be no density-dependent relationship for the stages of the life-cycle from the small larvae to the entrance into the population of the new adult. A similar result was found for the stage from the advent of the new adult through to the death of the adult. Thus the only part of the life-cycle left for a density-dependent factor to occur is the egg stage, which has a duration of only 6 days. During this stage a very marked density-dependent process takes place, the number of larvae hatching from eggs being greatly reduced as the density of adults increased.

The mechanism of this effect was examined and it appeared to be compounded of reduced egg-laying and increased egg-eating as the density increased. The algebraic sum of these two effects led to the observed result of a very rapid decrease in production of small larvae as the adult density increased.

It was suggested that the lack of competition over by far the greater part of the life-cycle may have a parallel in natural populations, where it is commonly asserted by field workers that competition appears to be low or non-existent. It was pointed out that *Tribolium confusum* populations, as natural ones appear to do, consume only a small fraction of their available food. If the control of natural populations involves similar processes then the density-dependent relationship must be sought for during a restricted part of the life cycle. Prof. O. W. Richards, Drs Solomon and Hynes took part in the discussion.

Miss Winifred E. Frost gave the last paper of the morning session, this being on 'The significance of the food relationships of fish in Windermere'. There are eight species of fish in Windermere, trout, char, pike, eel, minnow, stickleback and bullhead, with adult salmon as an occasional visitor. Although formerly this fish community was probably essentially a char-trout association, the present tendency is for pike and perch to predominate. An experiment, carried out since 1940, involving the drastic reduction of pike and perch, by traps and nets, is an attempt to alter the balance of fish populations again in favour of the char and trout. Some results of this experiment are relevant to the present discussion.

The foods eaten by the eight species show a fairly wide range of organisms but there is some overlapping of food requirements, therefore the possibility of inter-specific competition for food cannot be ignored. The only definite evidence on such competition comes through results of the perch reduction experiment. Perch, trout and char show considerable identity of feeding habit, so that with the perch reduced in numbers, it might be assumed that the remaining perch, also the trout and the char, would express the decreased pressure on food supplied by showing better growth or by increase in numbers; but that the perch have not in fact shown better growth suggests that competition is not a factor in the food

relationships of these species. Pike, large perch and large trout live almost entirely on other fish, the pike on perch, trout and char, the trout on perch and the perch on minnows. The pike is the chief such predator and the significance of food relationships in Windermere is most apparent from effects associated with the reduction in the numbers of pike. For, since this reduction, there has been a marked increase in the numbers of older and larger perch, a fivefold increase in the trout population, as estimated from seine nettings, and a great increase in the numbers of a population of breeding char.

On the evidence available it would seem that the primary significance of food relationships in Windermere lies in the predator-prey relationships of the fish-eating species.

A brief discussion followed in which E. D. Le Cren and Dr Turrill took part. The effect of angling on fish populations was discussed.

During the afternoon three papers were given. The first, by Brian Hopkins, was on the 'Species-area relationships of plant communities'. The object of this investigation was twofold: to investigate the species-area relations of plant communities, and to consider whether this information could be used to obtain an objective measure of certain ecological properties of plant communities.

The method used was to choose a uniform site of 20×20 m. from a plant community, and to sample within this using quadrats of different sizes. This enabled the mean number of species on areas from 0·01 sq.cm. to 400 sq.m. to be calculated. Twelve different types of British vegetation were studied.

The forms of their species-area curves were all very similar: after a rapid initial rise in the number of species with area, the rate of rise decreased with increase in area. The forms of their species-log, area curves were all similar; there was a slight increase in the number of species with increasing area for small areas, but the rate of increase became greater, and the curve became very steep on fairly large areas, where the number of species was approximately proportional to the logarithm of the area.

Very little evidence was found for the S-shaped species-log area curve proposed by some workers. The above results tend to support the view that the species-area relation is logarithmic. Curves of a logarithmic nature, 'α curves', have been fitted to the observed data and a reasonable fit was obtained. The ecological nature of the parameters used in the α curve equation was discussed. The 'index of diversity' (α) measured the diversity of the community and depended on the number of species present, and their type of distribution in that community. The α/N area was an objectively determined area of a plant community of extremely small size whose ecological meaning was not fully understood.

The concept of 'minimal area' was discussed and its determination from species-area and constancy-area curves. It was considered to be an unsatisfactory concept mainly because of the absence of a 'break' in these curves. Ecological 'pattern' and 'mosaic' were discussed with a view to objectively determining the size of the 'units' in this pattern.

In the discussion that ensued Dr Watt emphasized the importance of the biological approach to the study of 'pattern' and 'mosaic' in communities of plants. J. G. Skellam, Prof. Clapham, H. C. Gilson and Dr Hughes discussed various statistical aspects of the work.

A paper was then given by D. K. Dalby on 'Growth habit in *Salicornia*'. The annual species of *Salicornia* show considerable variation in size, and also in growth habit, varying from erect to fully prostrate. As these characters have been used in taxonomic work, it is necessary to consider the nature of this variation.

In the field, using a simple habit-grade scale, a parallel has been shown to exist between the annual *Salicornia* species and *Suaeda maritima* growing in the same habitat. Thus both are erect but simple in densely colonized salt-marsh pans, both attain maximum size on upturned mud dug from drainage cuts, and both tend towards the prostrate habit in saline fields and similar habitats.

Again, the presumably well-defined species *S. disarticulata* shows within its variation range for growth-habit, forms which have to be matched by three other supposed species of annual *Salicornia*, namely *S. ramosissima*, *S. prostrata* and *S. gracillima*. From this field evidence it is concluded that much of the variation in growth-habit and size in these plants is the result of response to the environment. It is unlikely that parallel selection of biotypes could occur in so many different localities, and in the short time that some of these habitats are in existence.

Experiment shows that some plants that are prostrate give wholly erect progeny, but not all prostrate habit is due to the environment, as one such plant gave progeny most of which were prostrate.

Plants which differ only in growth-habit, may grow so little as a foot apart, the one prostrate, the other erect. It is not easy to understand how the truly prostrate habit develops in nature if it is not inherited. It is not the same thing as the effect caused by plants being knocked down, when their apices grow abruptly erect again.

In the discussion that followed Mr Dalby stated in reply to Prof. Valentine that self-pollination was most likely in *Salicornia*. Drs Godwin and Goodman took part in this discussion.

P. Gay then gave the final paper of the meeting, this being on 'Lusitanian Ericads in Britain'. Mr Gay pointed out that the requirements of most of the Lusitanian species are not known, so that it is difficult to explain their present distribution or mode of introduction.

E. ciliaris L. only is considered here.

In Britain it has three noticeably disjunct areas, in Dorset, Devon and Cornwall. In Cornwall, where there is a tendency towards a drier habitat preference, its distribution is probably less natural than in Dorset, where there is a damper habitat preference. Morphological differences, at least in regard to corolla size and leaf shape, exist between the Cornish and Dorset populations. Hybridization with *E. tetralix* L. is thought to have contributed largely to the cause of this difference, and takes place probably largely due to man's action in breaking down the ecological barriers of the two species.

A hybrid index has been employed in the study of populations but is not sufficient. A new concept, that of Hybrid Number, is put forward. A graph of Mean Hybrid Index against Mean Hybrid Number for the populations, gives a rapid method for comparative work, and for the representation of the hybrid structure of the population. Some degree of discrimination between populations, according to habitat, can be achieved.

Within a short period of time, the consequences of hybridization are to enhance the variation of both species, producing new biotypes. This may have aided in the survival of many rare species. After a longer period of time, the rarer species will be absorbed into the wide ranging species, and in this way we may have lost some more Lusitanian species.

Despite hybridization, the two species have natural biological barriers keeping them as distinct foci of variation. Low fertility of hybrids and differences in flowering time of the two species are both important in this respect.

Dr H. G. Baker discussed the significance of a sterility barrier in the distribution of these species. Prof. Valentine and Prof. Clapham, and Drs Turrill and Clifford took part in this discussion. Dr Godwin referred to the possible period of entry of this Lusitanian Ericads into Britain, which might be about 7000–8000 years ago.

During this meeting Mr E. D. Le Cren, Honorary Secretary, read the auditors' account for the previous year (1953) on behalf of the Honorary Treasurer. The surplus of income over expenditure was nearly £574 due mainly to there being a small profit on the production of the *Journal of Ecology* instead of a substantial loss. The *Journal of Animal Ecology*, however, cost the Society over £466, but £267 of this was for the reprinting of Vol. 14 which is in short supply. Subscriptions, both for membership and to each of the *Journals*, were at new high levels. Once again the Society was indebted to the sales of back numbers of the *Journals* (£1450 altogether) for the favourable state of the finances.

At the close of the meeting the President from the Chair thanked, on behalf of the Society, all who had taken part in this meeting, and also to Prof. Pearsall for his hospitality and the continued use of the facilities of his department.

JOINT SUMMER MEETING WITH BRITISH PHYCOLOGICAL SOCIETY, ABERYSTWYTH

19–24 July 1954

Members assembled at Ceredigion Hall on the evening of 19 July and after supper were welcomed by Prof. Lily Newton on behalf of the Principal, Prof. Stephenson and the Warden of the Hall. The local secretaries, Dr Gwendolen Rees and Mr E. H. Chater then made some necessary financial and administrative arrangements.

On the 20th, two expeditions were made. The first and larger party—mainly consisting of botanists—went by bus to Mochras, near Harlech, where salt-marshes and sand-dunes were visited. Despite some damage due to the development of an aerodrome most of the plant communities could be demonstrated and a number of interesting plants were seen, including *Polygonatum odoratum* in dunes largely covered by bracken, *Ophioglossum*, *Selaginella* and *Petalophyllum ralfsii* in damp dune 'lows', *Salicornia perennis* and the recently arrived *Spartina townsendii* on the salt-marsh, and also considerable growths of dwarf *Fuci* and *Bostrychia scorpioides*. Tea followed at St David's Hotel, Harlech.

The second smaller, and more zoological party went by car after lunch to the Dovey estuary near Borth. Here Dr Watkin took the party down to the left bank of the estuary of the small Afon Leri. Digging in the mud and sand revealed a gradual increase in sandiness inhabited by successive species of lamellibranchs: *Scrobicularia plana*, *Mya arenaria*, *Cardium edule*, *Macoma balthica* and *Tellina tenuis*. As well as the molluscs some polychaetes and a burrowing isopod were collected. Collections in the river itself yielded various mysids and other shrimps, while in a ditch behind the sand dunes *Gammarus duebeni* was abundant, and *G. zaddachi* was taken from the *Fucus*-covered rocks in the R. Leri under the road bridge. The party then returned to the stream near the road bridge where among the *Fucus*-covered rocks *Gammarus zaddachi* and other crustacea were found. The party then enjoyed tea in Borth before returning to Aberystwyth.

In the evening members were entertained in the Department of Botany where various interesting exhibits were on view including herbarium specimens of seaweeds and pteridophytes, mutants of *Spartina townsendii*, predaceous fungi and an apparatus for photographing vegetation.

On Wednesday, the 21st, before the main excursion to St David's started, many members attended a talk by Dr J. R. Lewis in the Zoology Department when he described some of the basic features of the zonation of seashores, mainly as elucidated by the work of Prof. and Mrs Stephenson, and then discussed some of the problems particularly associated with the zonation on British coasts. An interesting discussion was cut short by the imminent departure of the bus to St David's. Brighter weather allowed us to enjoy good views of the scenery along the Cardiganshire coast, and we arrived at St David's at about 2 o'clock having had lunch in the bus en route. The party was then shown round St David's Cathedral by Canon Williams who gave us an interesting account of its main architectural and historical features. We then went down to the coast at White Sands Bay where an excellent *al fresco* tea was enjoyed among the sand-dunes. Members then spent two hours inspecting the rocks and collecting seaweeds and shore fauna. The inter-tidal zonation was clearly apparent and two main features of phycological interest were the bay with its boulders emerging from the sand, with *Gracilaria confervoides* dominant, and the rocky headland which forms a rich ecological habitat. On the headland, the rocks lie at a high angle, so that there are deep pools in the ledges between the strata. In these, lined by corallines, a number of other algae find a sheltered home. Species gathered included *Bifurcaria rotunda*, *Chylocladia ovalis*, *Taonia atomaria*, *Cystoseira ericoides*, *Cylindrocarpus berkeleyi* and *Griffithsia flosculosa*. Further out where oxygenation is very high, the Laminarias flourish and *Alaria esculenta*, *Himanthalia lorea* with *Elachista scutellata*, *Desmarestia ligulata* and *Nemalion multifidium* were found.

Thursday, the 22nd, was devoted mainly to Cader Idris, although some members went on a less energetic excursion up the Llyfnant Valley under the leadership of Prof. P. W. Richards, where many rare mosses and liverworts were seen and *Wahlenbergia hederacea* was in flower. The Cader party went by bus to Llyn Gwernan where they met Mr E. Price Evans, and then set off up the north side of Cader Idris. Half-way up Mr Price Evans gave a brief and lucid account of the geology of the district and described the main sites for the different types of flora in relation to the geology, and the excursion was made much more profitable and enjoyable by his presence. Lunch was eaten near Llyn Gafr and then in spite of dire warnings several of the party set out under the leadership of Mr Chater to climb over the summit of the mountain. Most of the party spent the afternoon exploring the basic volcanic outcrops above Llyn Gafr with their rich flora including *Meconopsis cambrica*, *Saxifraga hypnoides*, *S. oppositifolia*, *Thalictrum minus* subsp. *montanum* and various calcicolous mosses and lichens. The fine Cwm and moraine of Llyn-y-gader was also explored and many also went off to the north-east over the Nardetum and Callunetum towards Mynydd-y-Gader where a search for *Genista pilosa* was finally rewarded. Eventually all those who had stayed on the north side returned to the bus and drove to the south side of

the mountain where the party that had crossed over were safely collected for a welcome tea at Tal-y-Llyn.

The evening was spent in the Zoology Department, where Prof. Stephenson first of all showed us a collection of colour transparencies taken in Bermuda. The party then took coffee amongst a large display of exhibits showing the work in progress in the Department. These exhibits included many beautiful paintings and photographs of sea shores and their fauna and flora by Prof. and Mrs Stephenson, demonstrations on limpet ecology by Dr Lewis, the distribution of shore species by Dr Watkin, Welsh stream fauna by Dr Erichsen Jones, specimens and beautiful drawings of Helminth parasites by Dr Rees and some experimental work on colour change in the minnow and the reaction of small fish to toxic substances.

Friday, the 23rd, dawned wet but about two-thirds of the meeting went by bus to the western edge of Tregaron Bog. Here under the leadership of Mr Chater the small lagg was first examined where under the *Salix* carr several of the interesting species described by Godwin and Conway were found, including: *Menyanthes trifoliata*, *Potentilla palustris*, *Scutellaria minor*, *Carex pulicaris* and *Lotus uliginosus*.

The party then struck off across the main part of the bog while a few less stalwart members returned to the bus. Of special interest was the regeneration complex where all stages between hummocks dominated by *Calluna*, *Erica tetralix*, *Eriophorum vaginatum*, *Cladonia sylvatica*, etc., and hollows with bare peat under shallow water could be seen. Prominent in the further development of the latter were *Zygogonium ericetorum*, *Sphagnum cuspidatum*, *S. papillosum*, *Drosera intermedia* and *Eriophorum augustifolium*. After arriving at the other side of the bog and negotiating a bridge which was in an advanced state of decomposition the party went to Devil's Bridge where an excellent tea in some measure dispelled the dampness.

The other party spent the afternoon visiting the Welsh Plant Breeding Station at the invitation of the Director, and in spite of the rain enjoyed being shown interesting experiments in grassland improvement and the trial of new strains of grasses under the guidance of Messrs A. R. Beddows, Ll. Iorworth Jones and W. E. J. Milton.

In the evening the members were entertained to a reception in the University. Light refreshments were consumed while we listened to a recital of madrigals very effectively sung from the gallery of the hall. Afterwards most of us were able to enjoy a showing of the film taken by Professor Newton during her tour of Australia and New Zealand. Thus ended a most enjoyable and instructive meeting, which was evidently the result of most careful organization on the part of our hosts at Aberystwyth. The Society is most grateful to Prof. Newton and Prof. Stephenson, Mr Chater and Dr Rees and other members of the Botany and Zoology Departments, and the Plant Breeding Station, for the great trouble they took.

E. D. LE CREN

AUTUMN MEETING AT CAMBRIDGE

27–29 September 1954

The Autumn Meeting was held at the Botany School of the University, Cambridge, by courtesy of Prof. Briggs. Dr Godwin arranged for the accommodation of male members of the Society at Clare College. This was greatly appreciated.

The meeting opened with a soirée which was held in the Botany School. Dr Godwin and members of the University staff and research students had prepared a very extensive range of exhibits. These were very stimulating and provided much material for discussion during the evening. The pleasure of the evening was added to by excellent refreshments.

The following is a list of the exhibits:

A. S. Watt:	Fossil stone stripes and *Calluna* in Breckland.
H. Hamshaw Thomas:	Air-photographs of British vegetation from the Department of Aerial Photography, taken by Dr St Joseph.

E. J. H. Corner:	Some botanical illustrations.
S. M. Walters and F. Perring:	The working of the B.S.B.I. Distribution Maps Scheme.
E. A. George:	The Culture Collection of Algae and Protozoa.
S. M. Walters:	Plants in cultivation on the experimental plots of the University Botanic Gardens.
N. F. Robertson:	The pattern of mycorrhizal development in *Pinus*.
L. C. Frost and D. E. Coombe:	Heaths and soils on the Lizard serpentine.
Mrs H. L. K. Whitehouse:	Vegetation photographs.
E. Evans:	Recolonization of sterilized soil by micro-organisms.
R. West:	Interglacial pollen diagrams.
Miss S. Duigan:	The Brown Coal deposits.
K. Goodway:	The experimental taxonomy of *Galium pumilum* Murr. in the British Isles.
M. C. F. Proctor:	The habitats of *Helianthemum* spp. in the British Isles.

28 *September*. The morning meeting commencing at 10 a.m. was devoted to a group of papers which dealt with problems of plant-community classification.

Dr Duncan Poore opened the discussion with a paper on the 'Principles of Plant Sociology'. Dr Poore said that because of the growing divergence between the Continental phytosociologists and the Anglo-American ecologists an attempt was made to arrive at a compromise between their respective methods. Underneath their superficial differences the various phytosociological schools had a number of shared beliefs and practices: that vegetation units should be characterized and named in order that generalizations might be made from any studies on them; that these units were abstractions; and that they should be characterized floristically. The term NODUM was introduced to apply to an abstract vegetation unit of whatever rank; this corresponded with the term TAXON in taxonomy.

The method was based on describing chosen unit stands of vegetation, which should be uniform, and tabulating the descriptions of similar stands to produce noda. It was emphasized that choice was an essential part of the process, and that statistical methods of attacking the problem were inapplicable; uniformity was only a relative attribute of vegetation, but particular grades of uniformity could be distinguished for particular purposes.

The unit description should include, as a minimum: date, locality, altitude, aspect, slope, height and cover of vegetation, description of soil profile, area of stand and a list of all species present including bryophytes and lichens together with some measure of their cover.

The method was submitted to a field test in Breadalbane, Perthshire. It was found that vegetation units could be distinguished most satisfactorily by constancy and dominance—but not by fidelity, or by dominance alone. Evidence suggested that they could not be arranged in an hierarchical system such as Braun-Blanquet's but were related multi-dimensionally to one another.

The most useful feature of the method was not, however, in distinguishing and naming vegetation units for classification, but in using a precise survey method for the definition and partial solution of ecological problems. By the description of numerous unit stands correlation could be observed between floristics and habitat. Then, by successive approximations, the correlations could be so refined that the field for subsequent experimental confirmation might be greatly narrowed.

There followed a lengthy and interesting discussion of Dr Poore's paper. Dr Godwin outlined how, for many years he had felt that a closer understanding was necessary of the Continental system of plant-community classification and the study of plant sociology. Dr Poore's paper was undoubtedly an important contribution in this direction. Dr Godwin stressed the importance of the concept of 'noda'. Dr Watt stressed the great importance of understanding vegetation and the processes of changes going on within it. Dr Watt mentioned that many years ago he had used a similar system of listing plant communities to that used by Continental workers and now by Dr Poore. They, however, could not be included in the *Journal* of the Society due to difficulties of publication. Several members of the Society took part in the discussion including Profs. Osvald, Clapham and Webb, and Drs Walters, Gimingham, Hughes and Whitehead.

Mr F. H. Perring gave the last paper of the morning session. This was on the 'Ideal Vegetation Survey'. Mr Perring pointed out that Jenny has postulated that S, any particular Soil Type, can be expressed as a function of five independent variables, i.e.

$$S = f(cl, p, r, o, t),$$

where
cl = the regional climate,
p = parent material,
r = topography,
o = biological function,
t = time.

Major, in a paper in *Ecology*, 1951, has extended Jenny's arguments and suggests that V, the plant community, is a function of the same independent variables. Crocker in the quarterly *Review of Biology*, 1952, discussed the dependent and independent factors of vegetation at length and pointed out difficulties in assessing time zero for some factors. However, he concluded that no theoretical reasons convincing enough to challenge the basic ideas have yet been advanced, though it may be possible to apply the functional, factorial approach with absolute certainty to monogenetic systems only.

A study of chalk grassland has been used to test the functional factorial approach. V has been estimated quantitatively in different climatic regions. About sixty sites with similar management, undisturbed by ploughing (o and t constant) were chosen on different aspects at different angles of slope to give a network of points. The percentage cover of each species is plotted separately on an artificial hemisphere. Comparison of hemispheres for a species from different regions shows the effect of cl, the climate. Similar changes in rainfall can be compared in different temperature zones so that climate may be separated into two factors.

At a first analysis Chalk Grassland species fall into two groups. Those, relatively mesophytic, which are confined to N. and E. slopes in low rainfall regions, but have a wider spread in high rainfall regions, e.g. *Arrhenatherum elatius*, and the xerophytic species, most abundant on S.W. slopes at low rainfalls and tending to disappear at higher rainfalls, e.g. *Anemone pulsatilla*. Every gradation exists between the two extremes. On the basis of the hemisphere the species studied in Dorset were arranged in a series from most xerophytic to most mesophytic. Against these was plotted the change in constancy exhibited by the same species in going from 30 in. rainfall to 40 in. rainfall on Devonian limestone in Germany. There is a significant correlation. Local distribution reflects regional distribution.

It seems possible to isolate one factor by keeping others constant as far as possible, not only for plants but for soil. Comparison of rainfall gradients in different regions shows that with increased precipitation organic matter, Exchangeable P_2O_5, and Exchangeable Ca^{++} rise, while pH, and Exchangeable K^+ fall.

Mr Perring concluded that it will be possible to use the data to make similar studies on some of the other independent variables.

In the discussion that followed, Dr Watt, R. M. S. Perrin, Prof. Clapham and Dr Hughes took part. Mr Perrin pointed out the difficulty of ascertaining whether a chalk soil was contaminated with extraneous glacial drift or not, and that it was important to take this into account.

The afternoon session at 2 p.m. was opened by Dr R. E. Hughes who discussed the application of multivariate analysis to classificatory problems in ecology (this contribution represented joint work with Dr D. V. Lindley).

Dr Hughes showed how during his work in Snowdonia he had established an empirical system for classification of habitat types, based on (i) altitude, (ii) variation in local climate, (iii) soil parent material, and (iv) soil drainage conditions and related soil profile properties. The validity of the existence of these habitat classificatory units had to be examined. It was shown how in the case of thirty-six soil classificatory units established on the above basis (1) by the study of changes in soil properties in relation to an increasing rainfall gradient the number of classificatory units could be reduced to six; (2) subsequently by multivariate analysis these six units could be reduced to four.

The multivariate analysis technique that was used was that of Mahalanobis and Rao, which is based on the statistic D^2 (distance function) calculated from the means, variances, and covariances, of the quantities measured in two apparently different classificatory groups (the quantities here are four soil properties of Exch. Calcium, potassium, available P_2O_5 and pH). D^2 is a measure of the 'distance'

between the two groups, the larger D^2 is the more difference exists between the two groups, in terms of the quantities measured. D^2's between different pairs of groups may be compared. D^2 may also be used as a test of significance to see if any real difference exist between the two groups, based on the characters which have been studied (where only one character has been studied it reduces to the familiar Student's *t*-test). This may be extended to several groups and the D^2 relationship between six Snowdonia soil series have been worked out. The D^2 between two pairs was not significant and hence the six soil series could be tentatively reduced to four.

Dr Hughes also showed how this technique could be applied to problems of plant-community classification, since D^2 can be used as a coefficient of similarity between two communities. An example was given, where real differences between two communities were established based on the significance of the D^2 that was derived from quantitative data.

The application of multivariate analysis for discriminatory purposes was also discussed, both in soil- and plant-community classifications.

During the discussion, Dr Hughes pointed out, in reply to Mr Skellam, that the D^2 and canonical analysis reduced the multi-dimensional representation of the classificatory relationship to a more simple three-dimensional one. Prof. Webb, Prof. Clapham and Mr Chear also took part in the discussion.

Mr J. J. Donner then gave his paper on the 'Late-glacial vegetation of Scotland'. He pointed out that the correlation between the pollen analytical zones, the stages of ice retreat and the chronology based on varved clays and radiocarbon datings in north-western Europe forms the basis for the work in Britain. Here, as well as in Ireland, the late-glacial zones I, II and III have been demonstrated, but not the Bölling stage which preceded Allerød (zone II). On the other hand earlier interstadial stages have been found, e.g. in the Lea Valley north of London, and at Barnwell Station, Cambridge.

The northernmost late-glacial sites which have been investigated so far are Whitrig bog in southern Scotland, and Garscadden Mains near Glasgow, the latter by Mitchell. Besides these two sites three new sites with Allerød layers have been found; two in the area east of Loch Lomond and one in Keith, north-eastern Scotland. The pollen diagrams from these sites, as well as a new one from Garscadden, suggest that the vegetation during the Allerød period was open, in contrast to the park tundra further south in England. The tree-pollen content is 10–20%, consisting mainly of *Betula*, which, however, in some diagrams is *Betula nana*. *Salix*, in some cases *S. herbacea*, is regularly present. The vegetation in general was a late-glacial tundra with strong oceanic influence. Most common were sub-arctic *Empetrum-Calluna* and *Empetrum-Vaccinium* heaths, rich in herbs and grasses. Zone III is always represented by silts and clays formed by frost action. Late-glacial conditions still remained in the beginning of zone IV.

Drs Godwin, Clarke, Coombe and Gimingham, Mr Mitchell, and Prof. Webb took part in the discussion.

Dr Richard West, then followed with the final paper of the meeting on 'The interglacial deposits at Hoxne, Suffolk'.

The history of British vegetation since the end of the Last Glaciation is comparatively well known, but of the Pleistocene flora, and its changes related to the alternating glacial and interglacial climates of that period, much less is known.

Some evidence of it was described here. The interglacial beds at Hoxne were deposited between the two major glaciations of East Anglia, probably to be correlated with the Elster and Saale Glaciations of North Germany. They are lake deposits formed in a deep basin in the Lowestoft Boulder Clay, and are covered with sand and gravel of the later glaciation. The local topography has so changed since the time of the interglacial period that the lake deposits now lie on a ridge between two valleys.

Pollen analytical investigations of the lake deposits, which consist mainly of clay-mud and detritus-mud, give a record of vegetational history throughout nearly the whole of the interglacial. Four vegetational stages may be distinguished: first, a late-glacial stage characterized by the preponderance of non-tree pollen, especially *Hippophaë*, over tree pollen; secondly, a stage showing the immigration and development of mixed oak forest; thirdly, a change in this forest due to an increase in conifers, and finally an early-glacial stage with much sparser forest and with sub-arctic and arctic plants.

A very clear deforestation phase in the mixed oak forest stage was found, and it is interesting that this occurs at a similar level to the few Palaeolithic artefacts found in recent excavations. The presence of

charcoal at the same level suggests deforestation by fire, but whether natural or artificial it is impossible to say.

The vegetational types recognizable in the Hoxne Interglacial differ little from those found in the Late- and Post-glacial Periods in Britain. The only plants found at Hoxne and not now native to Britain are *Abies*, *Picea*, *Azolla filiculoides* and *Osmunda* cf. *claytoniana*. It seems that essentially the same flora invaded the glaciated parts of England after the second (Lowestoft) glaciation as after the Fourth or Last Glaciation.

In the discussion that followed Prof. Clapham and Prof. Webb, Mr Mitchell and Dr Godwin took part.

At 8.30 p.m. in the evening the Society again met at the Botany School where Mr V. C. Robertson showed an excellent series of colour photographs of the vegetation of Trans-Jordan.

He was followed by Prof. Hugo Osvald of Stockholm who gave a very interesting paper on the 'Vegetation of New Zealand peat lands'. This paper also was well illustrated with colour photographs.

A summary of this paper has been provided by Prof. Osvald and is reproduced here.

VEGETATION OF NEW ZEALAND PEAT LANDS

By Hugo Osvald

From 14 November 1951 to 1 February 1952 the author had the opportunity of travelling in New Zealand studying the peat lands. In particular my aim was to try to parallelize the New Zealand peat land types with those usually distinguished in north-western Europe.

Although the vegetation of New Zealand peat lands is quite different from that of the European ones, corresponding types may be distinguished.

The *flat fens* can according to Harris be classified in two groups:

(*a*) Fens with a vegetation dominated by trees and shrubs such as *Podocarpus dacrydioides*, *Cordyline australis*, *Coprosma tenuifolia* and *Hebe salicifolia*. These fens usually have a fairly low ground water-table and a shallow peat, and the trees may be rooted in the mineral subsoil.

(*b*) Fens with a vegetation dominated by herbs, sedges, rushes and grasses, such as *Typha muelleri*, *Phormium tenax* and *Carex secta*. These fens usually have a fairly high water-table.

Spring fens may occur in several places but only once was this type observed, i.e. at Wallaceville (near Wellington) at the margin of the main peat area. The vegetation was dominated by *Pratia angulata* in the field layer and *Breutelia* sp. in the bottom layer.

In a great number of cases in New Zealand it is difficult to decide whether a mire should be classified as a fen or as a bog. To some extent this seems to be due to the fires which counteract the development from fen to bog, in other cases to occasional flooding. Two examples may be mentioned:

The Okatirangi-bog, which is dominated by *Cladium teretifolium* sociation, *Schoenus pauciflorus* sociation and *Cladium glomeratum* sociation.

The great Hauraki plain swamp. The vegetation of this enormous peat area seems to be dominated by *Cladium teretifolium* and *Gleichenia circinata*. Hummocks of *Sphagnum* cf. *papillosum* are scattered over the surface. Other typical plants are *Hypolaena lateriflora* and *Drosera binata*.

Many of the large peat areas in New Zealand belong to the *raised bog type*. A good example is the Moanatuatua bog which is very conspicuously domed; there is, however, no lagg around the bog. The dominant plant community seems to be the *Cladium-Gleichenia-Campylopus* sociation, characterized in the first place by *Cladium teretifolium*, *Gleichenia circinata* and *Campylopus* cf. *retroflexus*.

Around raised bogs in New Zealand with one exception no laggs were observed. This might be explained by the presence of marginal forest—a common feature of New Zealand bogs—which may prevent the development of a lagg, owing to the amount of water transpired by the big trees, or the former presence of a lagg has been obscured by the reclamation of marginal areas for agriculture.

Bogs belonging to the *flat* (*margin*) *type* and the *concave type* seem to be rather common in the southern part of South Island. The Awarua-bog and the Waituna-bog east of Invercargill Mossburn-bog and Ramparts-bog may be classed in these groups.

The vegetation of these bogs differs in many respects from that of the raised bog. The most different type was studied on the southern part of Waituna-bog, close to the seashore. The dominant plant

community was the *Oreobolus strictus* sociation containing only a few species on the dense cushions of *Oreobolus*, among them *Gaultheria*, *Herpolirion novae-zelandiae* and *Celmisia* sp. The most striking feature was, however, the large mounds of *Donatia novae-zelandiae*. In this bog there is also a cyclic type of regeneration.

A bog which might be classed as intermediate between the *concave* and the *blanket bog* was studied at Swampy Hill near Dunedin, 2300 ft. above sea-level. The vegetation of this bog varied according to the grade (inclination) of the slope. On nearly flat areas the dominant community was the *Oreobolus* sociation with *Danthonia* sp. and *Dracophyllum* and narrow hollows with *Astelia* sp. On sloping ground *Danthonia* was dominant. In the steepest parts of the peat-covered slopes the peat was strongly wind-eroded.

In conclusion the following statement may be justified: Although there are great differences in vegetation between peat lands of north-western Europe and those of New Zealand, the same morphological types can easily be distinguished in both areas. It should be emphasized, however, that great differences exist in rather important details such as the laggs of the bogs and the regeneration cycles. This may be due to the fact that phanerogams play a much more prominent, *Sphagna* a much smaller, role in the peat formation on New Zealand bogs than on European ones.

29 *September*. Under the guidance of Dr H. Godwin the party visited Wicken Fen on Wednesday, 29 September, and were shown various stages in the primary hydrosere and of deflected successions associated with crop-taking. On the Main Drove the deposits of shell-marl (possibly Roman or post-Roman in date) were demonstrated, and on Adventurer's Fen in the excavations for the new mere, the party saw excellent exposures of the buried (Neolithic) oaks rooted on the underlying Gault Clay.

The Society is grateful to Prof. Briggs for granting the Society the use of facilities of the Botany School for this meeting. Also the Society is very indebted to Dr Godwin for organizing this meeting and the excellent arrangements which he made for both the soirée, the paper reading sessions and for the excursion to Wicken Fen. The Society is also grateful to the Masters and Fellows of Clare College for their kindness in placing the facilities of the College at the disposal of the Society.

R. ELFYN HUGHES

THE ANNUAL GENERAL MEETING

8 January 1955

The January meeting of the Society was held on 7 and 8 January 1955 at the Department of Zoology of the Imperial College of Science and Technology, South Kensington, by the kind invitation of Prof. O. W. Richards.

The meeting was well attended, eighty-eight members of the Society being present.

On the evening of 7 January, at 8 p.m., a soirée was held in the Department of Zoology. A number of exhibits were set out, which included two actinometers for solar radiation, illustrations of the ecology of a rock pool at Millport, and of the breeding of Atlantic seals. Prof. O. W. Richards's and Miss N. Waloff's work on the beetle *Phytodecta olivacea* was also illustrated. During the soirée a colour film of the Lough Ine rapids was shown by Dr J. A. Kitching. The quality of the colour film was excellent, and served to emphasize the potentialities of colour photography in ecological research.

The Annual General Meeting, 8 *January* 1955

The Annual General Meeting of the Society was held in the Lecture Theatre of the Department of Metallurgy. The morning session commenced at 10.30 a.m., the first part of the morning being devoted to the business meeting. Professor A. R. Clapham, the President, was in the Chair.

1. *Minutes of the last Annual General Meeting*

On the motion of the President, the minutes of the last Annual General Meeting (6 January 1954) were taken as read, since they had already appeared in *J. Ecol.* **42**, no. 2, pp. 579–85, and *J. Anim. Ecol.* **23**, no. 2, pp. 409–19.

The minutes were signed by the President.

Dr Hughes, the Honorary Secretary read the Secretaries' Report for the year. This report had been approved by the Council on the previous evening.

2. *Report of the Honorary Secretaries*

The thirty-fifth Annual General Meeting was held in the Department of Botany, The University, Sheffield, on 6 January 1954. A soirée was held on the previous evening at which a range of interesting exhibits were set out, dealing primarily with work in progress under Prof. Clapham, at Sheffield.

At 10.0 a.m. on 6 January the business meeting was held, under the chairmanship of Dr A. S. Watt, who acted in the absence of the President, Dr C. B. Williams. The proceedings of this business meeting have been reported upon in *J. Ecol.* **42**, no. 2, pp. 579–85, and *J. Anim. Ecol.* **23**, no. 2, pp. 409–19. During this meeting Prof. A. R. Clapham was elected President of the Society in succession to Dr C. B. Williams.

The paper reading session then followed at 11.0 a.m., which was devoted to a symposium on the 'Ecology of papyrus swamps in Uganda'. The Chairman was Prof. A. R. Clapham. The contributions were:

G. S. Carter: The aquatic environment of the swamps.
E. M. Lind: The swamp floras.
L. C. Beadle: Conditions in the mud below the swamps.

During the afternoon these papers were given:

J. C. Ritchie: Observations on the distribution of *Primula scotica* Hook.
F. H. Whitehead: Ecological significance of Alpine growth forms.
J. S. Colman and F. Segrove: The tidal plankton of a sandy beach.

The Society is indebted to Prof. Clapham for his hospitality and the excellent arrangements that he made for this meeting.

For the Easter Meeting on 2 and 3 April the Society again enjoyed the hospitality of Prof. W. H. Pearsall at University College, London.

Friday, 2 *April*

In the morning papers were read by:

E. Gorham: On the ionic composition of fen and bog waters, considered in relation to habitat and vegetation.
W. H. Pearsall: The bog surface as a dynamic system.
A. J. Rutter: Variation in the structure of a wet-heat community in relation to the water-table.

These further papers followed in the afternoon:

R. D. Hughes: Sampling the population of a Chloropid fly, in relation to the micro-climate.
E. M. Evans: Growth forms of Bryophytes in relation to successional and environmental change.
A. T. Clifford: The quantitative study of a hybrid swarm in the genus *Eucalyptus*.

In the evening at 8 o'clock a soirée was held in the Department of Botany, at which an interesting series of exhibits were set out.

Saturday, 3 *April*

In the morning the following papers were given:

P. W. Richards: Botanical impressions of Spain during the tenth International Phytosociologica Excursion.
W. H. Pearsall: Impressions of East African Vegetation.
J. Brereton: The factors controlling *Tribolium confusum* populations.
Winifred E. Frost: The significance of food relationships of fish in Windermere.

The final session was held in the afternoon, during which these papers were given:

B. Hopkins: Species area relationships of plant communities.
D. K. Dalby: Growth habit in *Salicornia*.
P. Gay: The Lusitanian Ericads in Britain.

During this meeting Mr E. D. Le Cren the Honorary Secretary read on behalf of the Honorary Treasurer, a short statement of the accounts of the Society for the previous year. The surplus of income over expenditure was nearly £574 due mainly to there being a small profit on the production of the

Journal of Ecology instead of a substantial loss. The *Journal of Animal Ecology*, however, cost the Society over £466, but £267 of this was for the reprinting of Vol. 14 which is in short supply. Subscriptions both for membership and to each of the *Journals*, were at new high levels. Once again the Society was indebted to the sales of back numbers of the *Journals* (£1450 altogether) for the favourable state of the finances.

The society is again very indebted to Prof. Pearsall for his continued hospitality.

The Summer Meeting was held at Aberystwyth on 19–24 July. This being a joint meeting with the British Phycological Society. On the 20th the botanists visited salt-marshes and sand-dunes at Mochras, near Harlech, while the zoologists examined the zonation of Lamellibranchs and other fauna in the Dovey estuary. The 21st was devoted to a trip to St David's where, after inspecting the cathedral, the late afternoon was spent among the intertidal zones of the rocky coast. On the 22nd most of the party spent an interesting day on Cader Idris where, under the guidance of Mr Price Evans, the geological and floristic features were clearly seen. A few members spent a less energetic day in the Llyfnant Valley. The next day in heavy rain Tregaron-bog was visited; here the regeneration complex of hummocks and pools was of especial interest. Another party inspected the Welsh Plant Breeding Station. The evenings were fully catered for by demonstrations in the Zoology and Botany Departments and, on the 23rd, a reception in the University. Talks, illustrated by lantern or film, were given by Prof. Newton, Prof. Stephenson and Dr Lewis. The Society is grateful for the care and hard-work which went into the organization of the meeting, especially that by the local secretaries, Dr Rees and Mr Chater, and for the warmth of the Welsh hospitality it experienced.

The Autumn Meeting (27–29 September) was held at the Botany School, University of Cambridge, by courtesy of Prof. Briggs. Accommodation for male members of the Society was provided at Clare College.

The meeting opened on the evening of the 27th at 8.30 p.m. with a soirée at the Botany School. Excellent exhibits were shown by members of the University staff and research students.

On 28 September, the morning session was given to a group of papers dealing with various aspects of plant-community classification. The papers were:

M. E. D. Poore: Principles of plant sociology.
F. H. Perring: The ideal vegetation survey.
R. E. Hughes: The application of multivariate analysis to the classification of plant communities.

The latter paper was actually given in the afternoon. It was followed by two papers dealing with some aspects of Quaternary research carried out at Cambridge.

J. Donner: The vegetation of Scotland in the Late-glacial period.
R. G. West: The interglacial deposits at Hoxne, Suffolk.

At 8.45 p.m. in the evening the Society met again to hear two papers by:

V. C. Robertson: Colour photographs of the vegetation of Trans-Jordan.
Prof. Hugo Osvald: The vegetation of New Zealand peat-lands.

Both papers were excellently illustrated by colour photographs.
On 29 September members of the Society visited Wicken Fen.

The Society is very indebted to Dr H. Godwin for organizing this meeting and arranging for accommodation at Clare College.

During the year two parts of Vol. 42 of the *Journal of Ecology* has appeared. This volume consists of 650 pages, and includes 28 original papers and 18 book reviews. Eight accounts appeared of the Biological Flora of the British Isles, these being:

C. T. Prime: *Arum neglectum* (Towns.) Ridley.
R. W. Butcher: *Colchicum autumnale* L.
G. Scurfield: *Deschampsia flexuosa* L. (Trin.).
O. E. Balme: *Viola lutea* Huds.
Marie E. Phillips: *Eriophorum angustifolium* Roth.
J. C. Ritchie: *Primula scotica* Hook.
G. E. Blackman and A. J. Rutter: *Endymion nonscriptus* (L.) Garcke.
Verna Jones and P. W. Richards: *Juncus acutus* L.

Two parts of Vol. **23** of the *Journal of Animal Ecology* have appeared. This volume consists of 437 pages, comprising 19 original articles, 13 book reviews and abstracts of papers with a bearing on animal ecology in the British Isles.

During the year the membership of the Society has increased from 841 to 879,* that is by 38. Fifty-nine are actually new members, 21 having ceased membership due to resignations or have ceased to pay their subscriptions.

The analysis of membership is as follows:

Total	Receive *Ecol.* only	Receive *Anim. Ecol.* only	Receive *Anim. Ecol.* + *Ecol.*	Associate members	Honorary members
879	464	251	153	10	4

Distribution:		
	Home	627
	British Territory	137
	Foreign	115
		879

The report was accepted by the Society. Dr A. S. Watt thanked the Secretaries for the work which they had accomplished during the year.

3. *The Report of the Honorary Treasurers*

Mr V. S. Summerhayes then presented the report of the Honorary Treasurers. The final report will be presented probably at the Easter Meeting. The finances of the Society showed a favourable balance of approximately £336. Some of the sources of income of the Society were mentioned. About £1240 were derived from subscriptions, interest on investments amounted to £220, and the Index to volumes of the *Journal of Ecology* brought in £10. The working expenses of the Society were low. The two *Journals* of the Society cost approximately £770, while the Biological Flora (a successful year) cost the Society £230.

The Treasurer also reported the continued increase in the sales of the *Journals*, as more libraries and institutions were taking them. The substantial sale of back numbers continued, but not quite on the same scale as in the previous years.

Services rendered by the Cambridge University Press cost the Society £550. This would probably continue for another year, when costs of publications would probably increase. In view of this the treasurers mentioned that it may be necessary to raise membership fees after this year. The Society's membership fee had so far remained unchanged since before the war.

Dr Godwin, on behalf of the Society, thanked the Treasurers for their work during the year. He also proposed, and was seconded by Dr C. B. Williams, that the Freshwater Biological Association should receive the annual grant of £10. This was approved by the Society.

Mr Summerhayes proposed, and was seconded by Dr Watt, that the sum of £2. 2*s*. be paid to the Co-ordinating Committee for Nature Conservation. This was also approved by the Society.

The election of Messrs Ryland, Clift and Neal as auditors of the Society was proposed by Mr Summerhayes and seconded by Dr Hughes. This was approved by the Society.

4. *The Election of Officers and Members of Council*

On the motion of the President the following list of Council officers for 1955 was accepted by the Society:

Hon. Secretaries: R. Elfyn Hughes, E. D. Le Cren.
Hon. Treasurers: V. S. Summerhayes, C. E. Hubbard.
Hon. Editors: H. Godwin, H. C. Gilson.
Council:
Retiring 1956: H. G. Baker, A. Macfadyen, A. S. Watt, P. Holmes.
To retire 1957: C. Elton, N. A. Burges, V. Conway, N. W. Moore.
To retire 1958: H. B. N. Hynes, G. C. Varley, F. H. Whitehead, C. B. Williams.
To retire 1959: J. H. Barret, E. M. Burrows, D. E. Coombe, J. F. Hope-Simpson.
Hon. Assistant Editor: D. E. Coombe.
Hon. Editors of the Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards.

* Total at 24 Jan. 1955: figures amended since report was presented.

5. *The Report of the Honorary Editors*

(i) *The Journal of Ecology.* Dr Godwin reported that there was a satisfactory number of good quality papers available. There had been an increase in size of Vol. **42** which had absorbed some arrears, but it still took twelve months for a paper to be published. Dr Godwin appealed to contributors to be concise in their presentation of descriptive studies. He suggested that long descriptive lists of plant communities, etc., could be placed in a central reference library such as that of the Nature Conservancy. The microfilming of primary data was also suggested. A parallel was drawn with the position in geology where extensive detail regarding suites of rocks were available at a central library, only carefully selected instances of such descriptive material appearing in published papers. Contributors might seek advice about presentation before publishing. In discussion Dr Godwin stated that it was important that heads of departments should give the necessary guidance at time of publication.

Dr D. E. Coombe was thanked for the considerable help he had given to the Editors during the year. Dr Godwin referred to the increased membership of the Society. The membership fees (25*s.*) were still at a low level and therefore the *Journals* do represent very good value to members.

It was reported that the Society's printers and publishers wished to increase their publishing charges. This might involve an increase in both membership fees and subscription rates. A committee of the council were examining the position during the year, and considering the possibility of alternative means of publishing the *Journals.* However, such a change could not be contemplated very easily in view of the very high quality of the work of the Cambridge University Press.

The Index Volume to the *Journal of Ecology* was for the first 20 volumes only. It was suggested that another might be produced for subsequent volumes. There was also the question of reprinting some of the back numbers, which were virtually out of print. This was under consideration.

In the discussion that followed, Dr Hughes, Prof. Webb, Dr Godwin, Prof. Clapham, H. C. Gilson and Dr Conway took part. The need, for a more mature and concise presentation of ecological studies was emphasized, and also that for a central repository for detailed information.

Mr H. C. Gilson followed with his report on the *Journal of Animal Ecology.* He stated that Part 1 of Vol. **24** would be large, containing nine long papers and an increased number of abstracts which now covered a wider range. Mr Gilson reported that he received a number of papers of high standard from foreign contributors. He, however, selected from such papers only those which dealt with general ecological principles rather than those which were of limited regional interest.

A delay of 13–14 months was reported in the publication of contributions. Mr Gilson drew the attention of members to the instructions to contributors set out at the end of the *Journal.*

At the close of this report the President thanked both Editors for their reports and work during the year.

6. *The Report of the Honorary Editors of the Biological Flora*

Prof. P. W. Richards then reported on Biological Flora. Greater progress had been made this year (8 accounts being published, see *Hon. Secretaries* report for 1954) but this was still insufficient.

Mr E. D. Le Cren then gave a list of dates of meetings for the coming year.

29–31 March at Durham.

13–19 July Summer Excursion at Aberdeen. Latter half of September—London.

Annual General Meeting 1956—possibly Oxford.

At 11.30 a.m. Prof. David Valentine took the Chair. Prof. Clapham gave his Presidential Address which was entitled 'Autecology and the Biological Flora'.

Prof. Clapham discussed the importance of the biological study of individual species in explaining vegetation and vice versa. The ecologist in the field could present intricate and complex problems to be subjected to a laboratory analysis of the factors involved. This was analysis of causation at the first level, a deeper study was the task of the biochemist and biophysicist.

This kind of work meant the careful planning and control of experiments and the constant interchange of ideas, between the field and laboratory ecologist. Prof. Clapham envisaged the establishment of an

Ecological Institute for this kind of work. This would be equipped with phytotrons of the kind used by Went and his co-workers, for the analysis at this first level of the effects of different environmental factors, and combinations of them, on plant growth and reproduction.

Prof. Clapham illustrated his points with frequent reference to some of the work already published in the Biological Flora. He dealt in particular with factors affecting germination and the establishment of seedlings in the field, and with the setting of seed. The main factors mentioned were time (storage and dormancy), temperature (in particular its diurnal variation), light (photoperiodism), water, and the effects of the substratum. The existence in the soil of organic inhibitors and stimulations of germination was discussed. Some of these may be root exudates.

Prof. Clapham's address marked out an important phase in the present day development of ecology—that is the phase in which the subject is emerging from its initial qualitative and descriptive phase to that of a more precise quantitative analysis of vegetation and the factors affecting it. This development inevitably involves experimentation both in the field and in the laboratory. The President's address summarized and integrated in an elegant, and most stimulating manner the present stage of our knowledge in this field, and opened up new avenues for further inquiry.

The afternoon session was opened by Dr J. MacLeod who gave a paper on 'Field populations of Calliphorine Flies'. Carrion-baited traps placed within 100 yards or less of each other, in different types of vegetation cover may show marked differences in catch. Bait traps can thus be used to determine the distribution pattern of the fly population, even over a limited area.

Serial trappings, for 5-day spells, were made at five sites over a 4-year period. They showed differences, both in the total densities and in the relative proportions of *Lucilia sericata*, the *L. caesar* group, *Calliphora erythrocephala*, *C. vomitoria*, *Phormia terrae-novae* and *Cynomyia mortuorum*, between open grazing fields, fields near hedgerows, rough mixed growth, and wood. The pattern of the population also showed seasonal changes, and consisted of *Calliphora erythrocephala* only in the very early and late phases of the fly season.

The overall picture for the fly season did not differ very markedly, in species composition, between a border upland sheep-grazing, an area of poor fell, a marginal mixed farming area, and a low-lying sheltered marsh in good mixed-farming country. The total density of calliphorines showed marked differences between the areas. The density was calculated by the Lincoln Index method, which, however, was found to have only limited application for blowfly populations.

Within the above areas, the distributions represented a mosaic of higher and lower densities, associated with the vegetational mosaic, and with topographic and edaphic differences. Within limited areas of apparently uniform ecological facies there was evidence of recognizable aggregations of the population. This was confirmed by unbiased sampling of the flies as normally distributed, i.e. not concentrated by the odour of bait. For this a tent-trap method was used in which a sq.m. of ground was covered at night by each of 100 tents, and the flies resting overnight on the covered vegetation recovered next day from the tents.

Flies, tapped in an area showing both vegetational and topographic diversity, were made radio-active and released at the mid-point of the area. With the exception of *Cynomyia mortuorum*, they were recovered up to the limits of the trapped area, i.e. over 1 mile away. The distribution pattern of recoveries bore no relation to the mosaic distribution of unmarked native flies of the different species, i.e. there is marked dispersive movement of individuals apparently without relation to the suitability of the terrain, or the grouping pattern of the species.

In the discussion that followed, Dr MacLeod in reply to Dr Watt stated that the effect of grazing animals could be ruled out. In reply to Dr Solomon it was stated that the quantitative data were not subjected to statistical analysis, but it was apparent that their variance was considerable. Prof. Cragg referring to his own work in this field, stated that he had observed mutual attraction and hence aggregation of individuals within the species. Therefore trap catches gave a different picture of the population. This, however, varies with season and altitude and changes occur with the maturation of the insect. Dr C. B. Williams referred to the reproduction of the pattern of distribution in two successive days. Dr MacLeod replied that he had little evidence of this kind.

Dr Orshan of the Department of Agriculture, Hebrew University, Jerusalem, then gave his paper on

the vegetation of Israel. Palestine is a meeting ground of different vegetation types belonging to three plant geographical regions. The Mediterranean, the Irano-Tauranian and the Saharo-Sindian. A fourth region—the Sudano-Decanian is represented by small enclaves only.

With mean annual rainfall varying from 25 to 1000 mm. for different parts of the country, falling only during winter, water is the most important among the habitat factors determining the distribution of plant communities. The border between the Mediterranean and the Irano-Tauranian territories is more or less delimited by the 300 mm. isohyet, while the 150 mm. isohyet separates the Irano-Tauranian from the Saharo-Sindian territories. The climax vegetation of the Mediterranean territory is an evergreen or deciduous forest or Maquis. At present, due to the destruction of the climax and soil erosion, the present-day vegetation is at different subseral stages.

The Irano-Tauranian territory bears more or less dense steppe vegetation.

The Saharo-Sindian territory bears desert vegetation. The leading species are dwarf shrubs and the total coverage does not exceed 10% in summer. As the minimal rainfall necessary to maintain plant life under the prevailing climatical conditions is about 50 mm., parts of this territory are devoid of vegetation.

The Sudano-Decanian enclaves are found within the Saharo-Sindian territory where the water-table is high. Thus the leading Sudano-Decanian trees get abundant water supply, together with high temperatures in the summer.

The morphological behaviour of the leading species and its bearing on drought resistance were briefly described. In the early summer the larger winter leaves of the dwarf shrubs are replaced by smaller summer leaves. This leaf change causes a reduction of the total water output by reducing the transpiring body 6–10 times. The Mediterranean trees, either evergreen or deciduous, do not show such a surface reduction during the summer.

This plasticity of members of the Israel flora was of considerable interest, and the subject of a lengthy discussion, in which Drs Gimingham, Turril and Ashby took part. Dr Turrill commented that the Irano-Tauranian phytogeographical region needed further subdivision.

The final paper of the meeting was given by Prof. O. W. Richards and Dr M. Waloff, this being entitled 'The study of a population of a beetle (*Phytodecta olivacea*) living on broom'. Miss Waloff who read the paper said that *P. olivacea* is a beetle about which almost nothing is recorded. There is an area at the Imperial College Field Station, Berks., with a considerable growth of broom on which the beetle is common. Since 1948 it has been used as an exercise in classwork on ecology, but recently a more detailed study of this species has been started.

The adults spend the winter in soil. They emerge at the end of April and begin to lay eggs. There are four larvae stages on broom, but pupation is in the soil. The second generation of adults appears in August; meanwhile the first generation die or enter the soil. The new generation feed, and then without pairing or laying enter the soil.

The weekly estimates of adults were based on beating a standard number of broom units or 'armfuls'. There are 4770 of these in the area, the green parts of each unit weighing about 300 g. These estimates were on some occasions checked by marking and recapturing the beetles. The total in each generation was obtained by dividing the accumulated total of weekly estimates by the average time spent above the ground; this time was determined in cages. The number calculated for the first generation was 11,170 and 32,080 for the second. The figure of 11,170 was checked by a second estimate of the calculated number emerging in forty enclosed areas; this gave the total of 8920 beetles. The combined total of 43,250 beetles in the field was checked in November, by taking soil samples under broom. These gave an estimate of 45,120, 66% of which were dead.

The numbers of eggs and larvae in weighed broom samples were related to the amount of broom in the field. The totals of various stages were again divided by the duration of each stage, determined in the laboratory.

A little is known about the causes of mortality, but not in a quantitative way. The eggs are eaten by a number of Heteroptera. The larvae are parasitized by a Tachinid fly *Meigenia*. A large number of adults in the soil are killed by a fungus akin to *Entomophthora*, they also contain Hymenopterous, Braconid larvae, which have not yet been identified.

The errors involved in the quantitative work were discussed by E. D. Le Cren, J. G. Skellam, Dr J. McLeod and Dr C. B. Williams. Such factors as size of sample and mobility of insects were considered.

At the close of the meeting Prof. Clapham from the Chair thanked our hosts, Prof. Richards and his staff, for their hospitality and the excellent arrangements they had made for the meeting, which had ensured its success.

NOTE. At a meeting of the Council of the British Ecological Society on 7 January 1955 it was agreed that the above account of the Annual General Meeting was to stand as *unconfirmed minutes* of that meeting, and these to be presented for confirmation at the next Annual General Meeting, and that this practice should be continued in future years.

R. ELFYN HUGHES

LIST OF MEMBERS (24 JANUARY 1955)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, R. E. HUGHES, The Nature Conservancy, c/o School of Agriculture, University College of N. Wales, Memorial Buildings, Bangor, Caernarvonshire.

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